Island Arc

WILEY

Island Arc

RESEARCH ARTICLE OPEN ACCESS

An Ordovician Assemblage of Cool Water-Adapted Paleotropical Ostracods Suggests an Early Psychrosphere

Anna McGairy[1,2] | Phong Duc Nguyen[3] | Mark Williams[1] | Christopher P. Stocker[1] | Thomas H. P. Harvey[1] | Toshifumi Komatsu[4] | Thomas W. Wong Hearing[1] | C. Giles Miller[2] | Chloé M. Marcilly[5] | Alexandre Pohl[6]

[1]School of Geography, Geology and the Environment, University of Leicester, Leicester, UK | [2]Department of Science, Natural History Museum, London, UK | [3]Department of Paleontology and Stratigraphy, Vietnam Institute of Geosciences and Mineral Resources, Hanoi, Vietnam | [4]Faculty of Advanced Science and Technology, Kumamoto University, Kumamoto, Japan | [5]Centre for Planetary Habitability (PHAB), University of Oslo, Oslo, Norway | [6]Biogéosciences, UMR 6282 CNRS, Université de Bourgogne, Dijon, France

Correspondence: Anna McGairy (am1220@le.ac.uk)

Received: 13 February 2024 | **Revised:** 14 October 2024 | **Accepted:** 21 November 2024

Funding: This work was supported by the Institut National des Sciences de l'Univers, CNRS (Programme TelluS, project ROSETTA); The Leverhulme Trust (RF-2018-275/4, RPG-2022-233); Agence Nationale de la Recherche (ANR-22-CE01-0003); the Vietnamese project "Research and investigation of the scientific value of geological heritage in some newly opened or expanded road sections to contribute to the preservation and promotion of the value of Dong Van Karst Plateau UNESCO Global Geopark", (ĐTCN.HG-04/2023); Natural Environment Research Council, UK (NE/S007350/1); Japan Society for the Promotion of Science (16K05593, 19K04059); and the Vietnamese project "Research of the paleoclimatic and paleoenvironmental conditions for the Cambrian sedimentary rocks at typical geoheritage sites in North Vietnam", (TNMT.2023.562.12).

Keywords: biogeography | climate simulations | Ordovician | ostracods | psychrosphere | Vietnam

ABSTRACT

An ostracod assemblage from the Late Ordovician (Katian) Phu Ngu Formation of northern Vietnam, South China paleoplate, yields typical Baltic and Laurentian-affinity genera together with some endemic forms. Detailed paleontological and sedimentary analysis of the Phu Ngu Formation suggests it was deposited in a deeper marine forearc setting, below storm wave base, but with (at least intermittently) oxygenated sea-bottom conditions. Taphonomic assessment of the ostracod assemblage suggests it is in situ. The occurrence of globally widespread ostracod genera, including those from paleocontinents that were geographically remote from South China, is difficult to reconcile with the assumed limited dispersal capability of ostracods in shallow-shelf settings—a characteristic that has often been used to refine Ordovician paleogeographical reconstructions. Here, we present the novel approach of using paleoclimate reconstructions to assess the environmental distributions of Paleozoic ostracod genera. We show that the deep-marine depositional setting of our documented assemblage, together with general circulation model simulations of Ordovician ocean-temperatures, suggests an early radiation of benthic ostracods into the deeper, colder, and thermally uniform ocean below the thermocline. The presence of a globally-distributed psychrospheric (cool and deep marine) ostracod fauna would imply that our understanding of Ordovician ostracod dispersal is incomplete, and future paleobiogeographical studies should try to decouple the signal of shallow-shelf benthic taxa, often endemic and probably limited by sea temperature, from those that are more cosmopolitan and tolerant of cooler, deeper waters.

1 | Introduction

Detecting the existence of deep ocean benthic assemblages in the early Paleozoic is often limited by an absence of preserved deep ocean sediments and their contained fossil biota. Nevertheless, the distributions of some benthic marine taxa suggest there must have been deep ocean connections between distant paleocontinents, including trilobites (e.g., Ebbestad and

Fortey 2019; Stocker et al. 2019) and brachiopods (e.g., Cocks and Torsvik 2021). Here, we use the global distribution patterns of Ordovician ostracods, coupled with evidence of a cold water-adapted tropical assemblage from northern Vietnam and climate simulations of Ordovician oceanography to infer the presence of a deep water, psychrospheric ostracod fauna in the early Paleozoic.

Modern ostracods inhabit a wide range of aquatic environments, but the earliest ostracods are generally considered more restricted in their ecologies. Ostracods of the Subclass Podocopa were widespread in marine shelf environments by the Early Ordovician (Tremadocian; Salas and Vaccari 2012; Williams et al. 2008). Like all modern podocopes, Ordovician representatives of the Podocopa (e.g., palaeocopids, binodicopids and leiocopids) are assumed to have been benthic, lacking a pelagic larval stage. It is only within the Subclass Myodocopa, which originated as benthic ostracods in the Late Ordovician (Gabbott et al. 2003; Siveter et al. 2014), that the pelagic mode of life evolved by the late Silurian (Perrier, Vannier, and Siveter 2011; Siveter et al. 2010; Siveter, Vannier, and Palmer 1991). All Ordovician ostracods are thought to have exclusively inhabited marine environments, including shelf settings (e.g., Mohibullah et al. 2012; Vannier, Siveter, and Schallreuter 1989) and more proximal settings with variable salinity (e.g., Williams and Siveter 1996). It is not until the late Silurian (Pridoli) that they are known to colonize estuaries (McGairy et al. 2021), and only by the Carboniferous are they recorded from freshwater settings (Bennett 2008; Bennett et al. 2012).

The apparent restriction of Ordovician podocope ostracods to marine shelf environments has enabled the taxonomic similarities and differences of fossil ostracod faunas to be used to test reconstructions of plate-tectonic evolution. For example, similarities in faunas from the Ordovician of North America and western Europe have been used to suggest the narrowing of the Iapetus Ocean during the Late Ordovician and the movement of the Baltica and Avalonia paleocontinents into the paleo-tropics (Schallreuter and Siveter 1985; Williams et al. 2003b). Other studies have used early Paleozoic ostracods to examine the development of the Rheic Ocean (Vannier, Siveter, and Schallreuter 1989); to indicate marine paleodepth (e.g., Siveter 1984); and to explore regional patterns of paleoenvironment (e.g., Ainsaar and Meidla 2001; Jaanusson 1976; Mohibullah et al. 2012).

Here, we describe new material from the Upper Ordovician Phu Ngu Formation of northern Vietnam. We report a mixed podocope ostracod assemblage of genera that are endemic to the South China paleoplate alongside those that are more cosmopolitan, including from paleocontinents such as Laurentia and Baltica that were geographically remote from South China in the Ordovician (Cocks and Torsvik 2021). The prevalence of cosmopolitan genera, combined with their large geographical distribution ranging from low to polar latitudes and their presence in overall deep-water sedimentary facies, raises questions about the patterns of migration of Ordovician ostracods and whether the distribution of these faunas may represent evidence for a paleopsychrospheric community. Today, the psychrosphere represents water masses below the thermocline with temperatures $<10°C$, with depths ranging from 700 m to as shallow as 100 m in regions where there is strong upwelling (Bruun 1957). By implication, equivalent water masses can be expected to have been present in the geological past, dependent on the climate state. The presence of a deep-marine, psychrospheric benthic ostracod fauna in the Ordovician could challenge the biogeographical utility of some ostracods by implying an incomplete understanding of their dispersal mechanisms.

A psychrospheric ostracod fauna evolved several times through the Phanerozoic (Crasquin and Horne 2018); the modern psychrospheric ostracod fauna was established in the Cenozoic (Benson 1988) and today ostracods are known to inhabit psychrospheric waters from the depth of the thermocline to the deep abyssal oceans (Brandão et al. 2019; Brandt et al. 2019; Jellinek, Swanson, and Mazzini 2006). In the Paleozoic, a distinct ostracod fauna comprising several taxa with prominent spines and thin shells known as the Thuringian Ecotype or Mega-assemblage (Bandel and Becker 1975; Zagora 1968) has previously been suggested to represent a paleopsychrospheric fauna (Kozur 1972, 1991), though some authors instead view it as more generally representative of low-energy environments (Becker 2000; Becker and Bless 1990; Becker, Clausen, and Leuteritz 1993). Crasquin and Horne (2018) identified a Devonian psychrospheric ostracod fauna and suggested that the long-term survival of the Thuringian Mega-assemblage (Late Ordovician—Middle Triassic; Becker 1982) could be attributed to the paleopsychrosphere providing a place of refuge during the Late Devonian and end-Permian mass-extinction events (see also Benson 1988).

To test whether the Phu Ngu ostracod assemblage represents a cold water-adapted fauna in the tropics, that is, living within thermocline depths, we examine the sedimentological and paleoenvironmental setting of these ostracods and attempt to determine their taphonomy and taxonomic relationships. We use evidence from the Phu Ngu ostracod assemblage, coupled with a global analysis of Ordovician ostracod faunal distribution, and climate simulations for the state of the oceans, to test for a signal of a psychrosphere in the early Paleozoic. We also consider how different oceanographic factors may have influenced the distribution of ostracods.

2 | Geological Setting

Northern Vietnam was part of the South China paleoplate during the early Paleozoic (Figure 1; Cocks and Torsvik 2013; Isozaki 2019). Within northern Vietnam, three geotectonic zones are defined, each displaying its own lower Paleozoic lithostratigraphical signature (Tong et al. 2013). The ostracod material described here is from the East Bac Bo Zone, which is bound to the south and west by the West Bac Bo Zone (separated by the Song Chay Fault), and to the east by the Quang Ninh Zone (Tong et al. 2013). The Upper Ordovician Phu Ngu Formation crops out regionally in the East Bac Bo Zone and comprises predominantly siliciclastics, approximately 2.3 km to 2.4 km thick at the type section (Tong and Vu 2011). The Phu Ngu Formation was deposited in a deeper marine island arc setting on the slope of the Paleo-Tethys Ocean during the Late Ordovician and Silurian (Tong et al. 2013; Tong and Vu 2011). The formation crops out in the Na Ri District in exposures of gray, greenish-gray, and beige mudstones and sandy mudstones, interbedded with infrequent

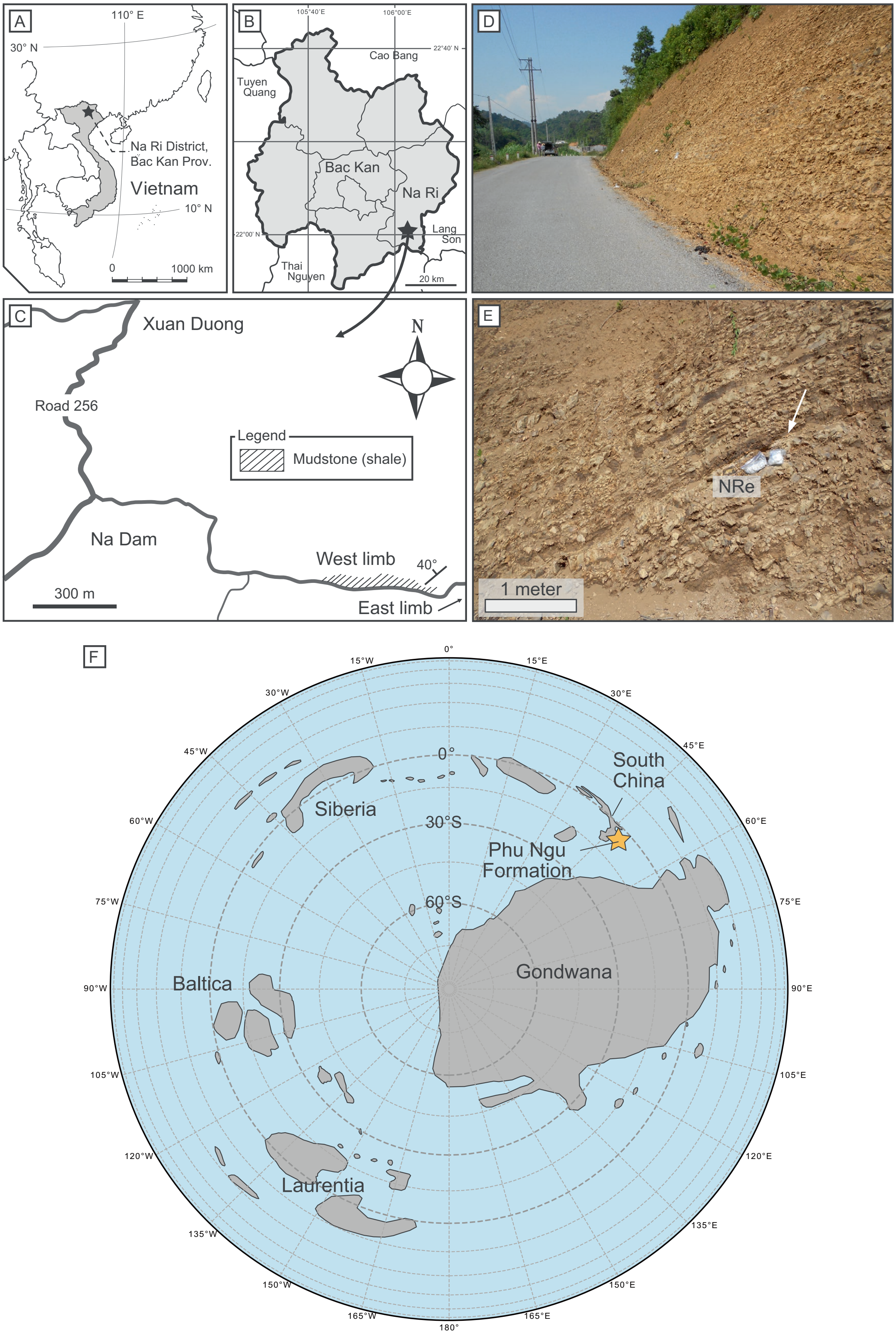

FIGURE 1 | Study area location and paleogeographic context. (A) Map of Vietnam (gray shading), showing Bac Kan Province and the Na Ri District (star); (B) Bac Kan Province (gray shading) with Na Ri District highlighted (star); (C) map with locality and exposure; (D) road cutting of the Phu Ngu Formation; (E) close-up of the exposure of the Phu Ngu Formation in the Na Ri District. Arrow points to bentonite bed, directly below which are sample bags on horizon NRe; and (F) global paleogeographic reconstruction for the Katian (Late Ordovician) showing the position of the Phu Ngu Formation on the South China paleoplate, Lambert azimuthal equal-area projection, centered on the South Pole.

volcanic ash layers (Figure 1D,E), with a suggested thickness of ~250 m in this area (Tong et al. 2013; Tong and Vu 2011).

The macrofossils found with the ostracods are conulariids, orthocones, brachiopods, graptolites, and trilobites (Wong Hearing et al. 2021b). These are sparsely distributed through the succession. Previous work on the Phu Ngu Formation identified the early Katian *Dicranograptus clingani* graptolite Biozone (Wong Hearing et al. 2021b), from taxa at different horizons including *Normalograptus daviesi* and *Dicellograptus flexuosus*. Other graptolites from the Phu Ngu Formation in this area include species of *Climacograptus*, *Orthograptus*, and the dendroid *Dictyonema*, though the latter is not from the ostracod-bearing horizons (Wong Hearing et al. 2021b). Regionally, the Phu Ngu Formation yields graptolites of Late Ordovician (Katian and Hirnantian ages) and early Silurian age (Nguyen 2002; Tong et al. 2013; Tong and Vu 2011; Wong Hearing et al. 2021b).

Wong Hearing et al. (2021b) interpret the mixed graptolite and shelly assemblage in their "Locality 2" as being deposited in a marine shelf setting, due to the presence of palaeocopid ostracods (cf. Vannier, Siveter, and Schallreuter 1989; Williams et al. 2003b). The graptolite fauna including *Dicellograptus* suggests oceanic influence (e.g., see Williams et al. 2003a), and corroborates a deep marine shelf or slope setting. The sedimentological and geotectonic setting of the Phu Ngu Formation in Na Ri resembles that of the Late Ordovician succession in the Girvan area, southern Scotland, where mixed graptolite and ostracod assemblages are known from a fore arc setting on the paleocontinental margins of Laurentia (Floyd, Williams, and Rushton 1999; Mohibullah et al. 2011).

3 | Materials and Methods

3.1 | Fieldwork

Material was collected over two field seasons in northern Vietnam during autumn 2018 and 2022. The fossils were recovered from a roadside exposure near Na Dam (Figure 1), close to the "Nazam" Section 25 of Nguyen (2002), in the Na Ri District. In 2018, two localities were sampled and described for their graptolites by Wong Hearing et al. (2021b). Subsequently, the construction of a new road section resulted in the 2018 localities being buried beneath road fill. However, a new road cutting identified in October 2022 exposes a comparable and along-strike succession (Figure 1D,E), with stratigraphic equivalence supported by graptolite biostratigraphy. Material from both sections is examined here. In total, 10 horizons were sampled from the 2022 road cutting (Figure 2), with more than 60 slabs yielding over 700 ostracod specimens, of which around 90 are identifiable at species-level. An additional 25 identifiable ostracod specimens are included from the 2018 material, from "Locality 2" of Wong Hearing et al. (2021b).

3.2 | Laboratory Analysis

The ostracod-bearing strata comprise fossiliferous beige-colored sandy mudstones and siltstones. The deposits were examined both in hand specimen and thin section. The ostracods are predominantly preserved as either external or internal molds (Figure 3), although rare, decalcified valves are found. Most specimens are complete but disarticulated, with only occasional fragmentation. Ostracod specimens are distributed sporadically throughout the formation, with occasional shell lag concentrations of both ostracod and associated macro-faunal fragments. Thin sections

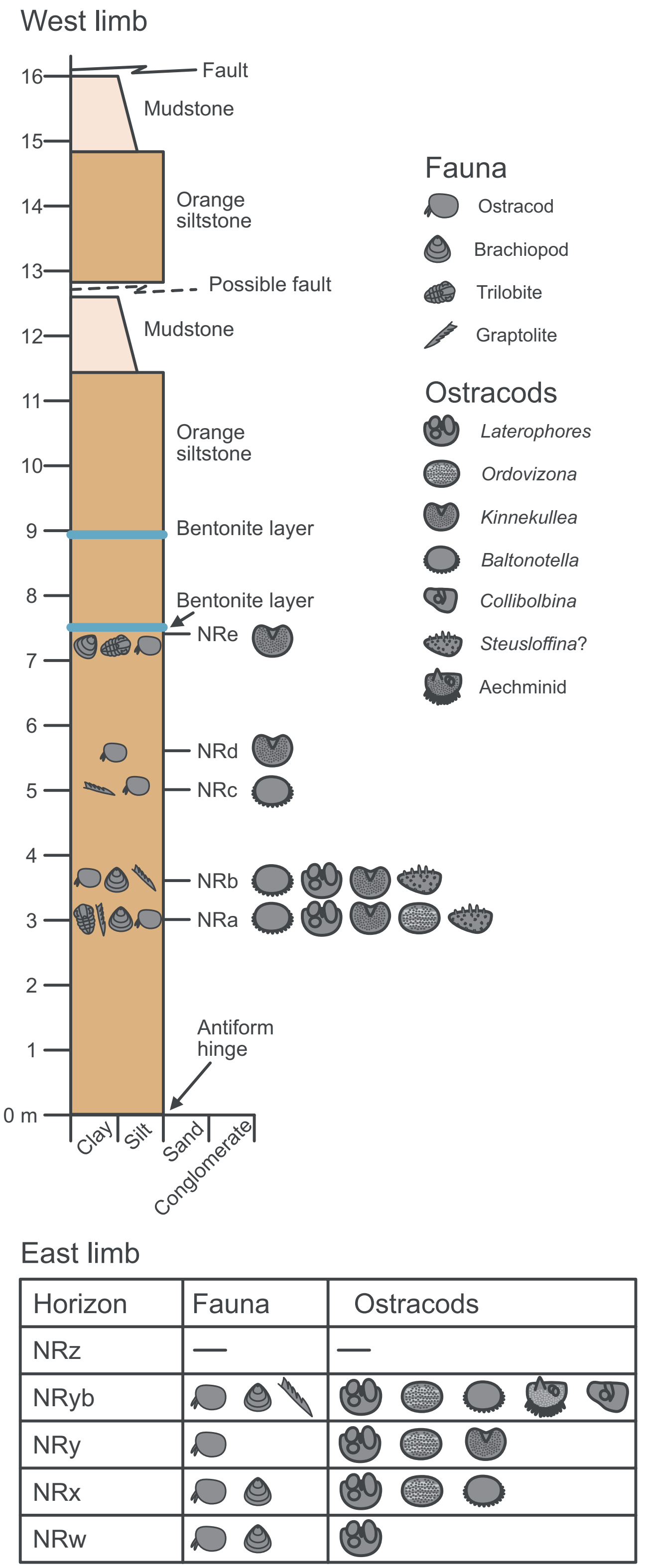

FIGURE 2 | Stratigraphic log of the west limb of the anticline accessible in the Na Ri district section of the Phu Ngu Formation (top) and table showing the distribution of fauna and ostracod taxa recovered from the horizons of the east limb (bottom).

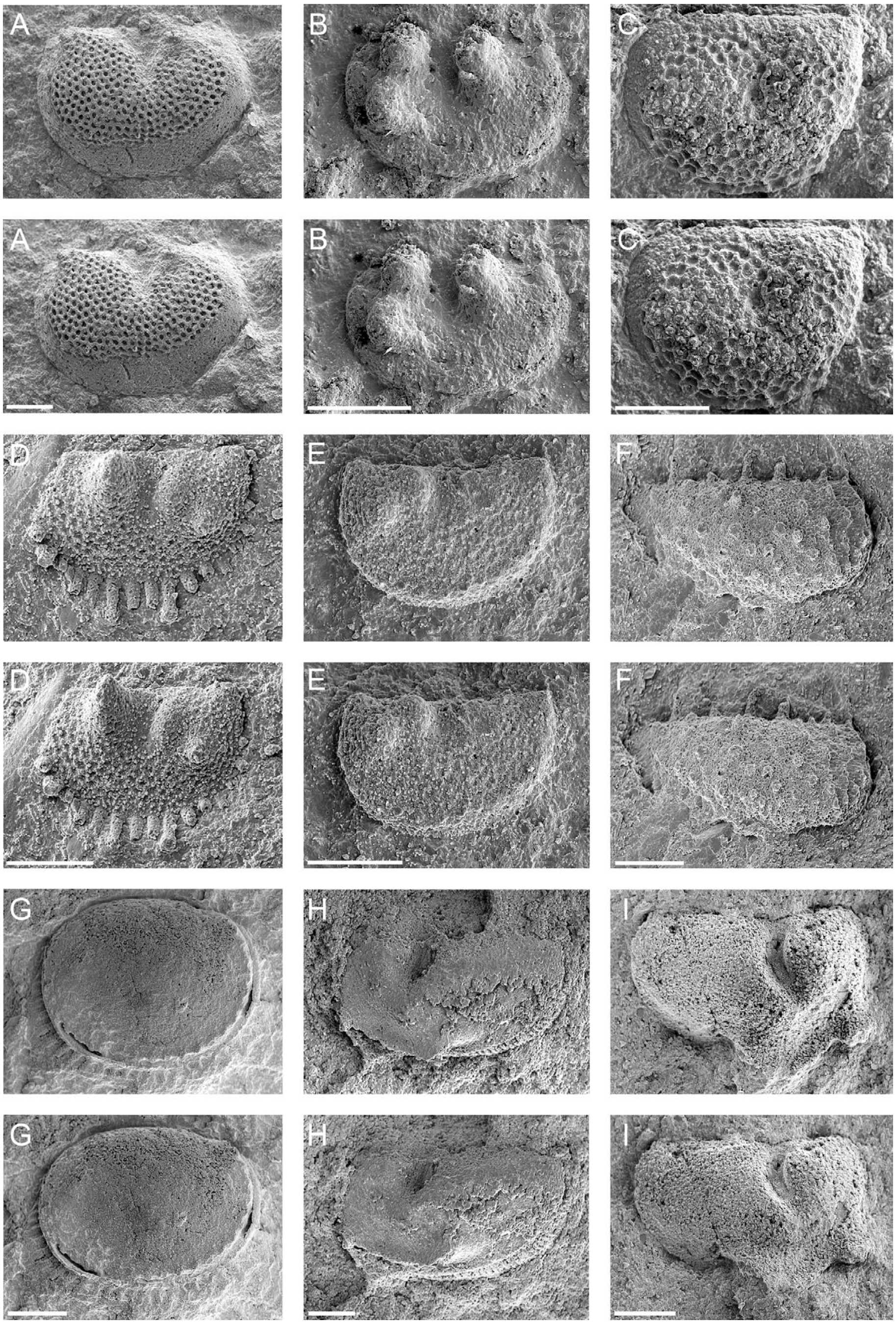

FIGURE 3 | Ostracods of the Phu Ngu Formation, all presented as scanning electron micrograph stereopairs from silicone rubber casts of external molds; all scale bars 200 µm. (A) *Kinnekullea gaia* Wong Hearing et al. 2021b (VNMN.0190c part); (B) *Laterophores* sp. A (=*Laterophores* sp. of Wong Hearing et al. 2021b; VNMN.0182L part); (C) *Ordovizona* sp. (=*Ordovizona*? sp. of Wong Hearing et al. 2021b; VNMN.0167b); (D) Aechminid sp. (VNMN-P-6208L); (E) *Laterophores* sp. B (VNMN-P-6197a); (F) *Steusloffina*? sp. cf. Zhang (2023; VNMN-P-6184d); (G) *Baltonotella* sp. (VNMN.0164d); (H) *Collibolbina* sp. (VNMN-P-6188b); and (I) *Collibolbina* sp. (VNMN-P-6191a).

were examined using petrographic microscopy under both transmitted and reflected light (Figure 4).

"Silcoset 101" was used to make silicone casts of the external molds, which were then sputter-coated with gold and imaged using a Hitachi S-3600N environmental scanning electron microscope (SEM) at the University of Leicester. Specimens were consolidated using a solution of 1% "Paraloid B72" in acetone before casting. When casting, specimens with spines or fine ornamentation were left to set in a pressure chamber at 2-bar overnight to prevent bubbles forming in the silicone casts. Specimens figured here are curated in the collection of the National Museum of Nature, Hanoi (prefix VNMN).

3.3 | Data Compilation

To examine the broader chronological (Figure 5), paleoenvironmental and paleobiogeographical significance of the ostracod fauna in the Phu Ngu Formation, data have been compiled for

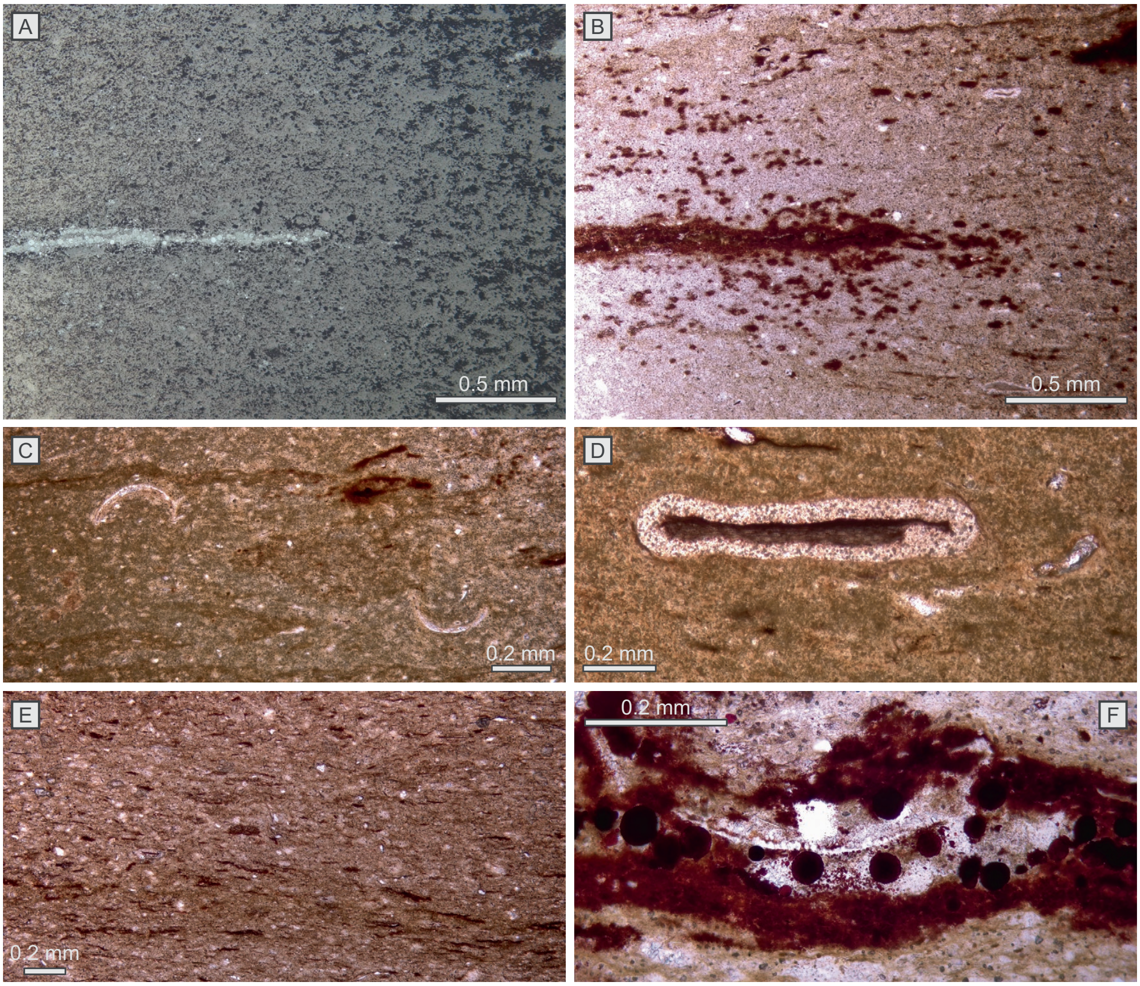

FIGURE 4 | Thin sections of the Phu Ngu Formation deposits. (A) is reflected light, (B–F) are plane-polarized light. (A, E) Sedimentary texture, including a lens of pyrite framboids in (A); (B, D) agglutinating benthic foraminifera, (B) is the same field of view as (A); (C) ostracod valves; and (F) fragment of shell (possibly ostracod) associated with pyrite framboids.

the global distribution of species of *Kinnekullea*, *Laterophores*, *Baltonotella*, *Collibolbina* and *Ordovizona* (Table 1, and Table S1), all of which are genera that are known from geographically distant Ordovician paleocontinents relative to South China, such as Baltica and Laurentia. Data were compiled from multiple published sources and occasionally from unpublished theses (Orr 1987; Williams 1990). These include species identification, lithostratigraphical and chronostratigraphical context, paleogeography including calculated paleo-coordinates, and paleoenvironmental context including an assessment of marine water depth. Where the marine depth is not explicitly discussed in a paper, this is inferred from sedimentological and paleoenvironmental interpretations (see Table S1).

3.4 | Paleogeographic Analysis

Paleobiogeographic reconstructions of the Ordovician were produced following the paleogeographic reconstructions of Marcilly et al. (2021), which, in turn, are based on the plate reconstructions of Torsvik and Cocks (2016). Marcilly et al. (2021) inferred the extent of exposed land from a combination of lithofacies and paleoclimatic reconstructions at 10 Myr intervals. A hypsometric slope is not calculated for each continent separately (Marcilly, Torsvik, and Conrad 2022), so variations in the steepness of marine shelves are not considered in this model. As the temporal uncertainty for each map is ±5 Myrs (Marcilly et al. 2022, 2021), the most appropriate 10 Myr interval map was used for each chronostratigraphic age represented in this study: 460 Myr for the Darriwilian, 450 Myr for the Sandbian and the Katian, and 440 Myr for the Hirnantian. Ostracod paleobiogeographic maps were reconstructed for each chronostratigraphic stage by paleo-rotating the locations of fossil ostracod occurrences using GPlates through the Python module GPlately (Table S1; Mather et al. 2024). The age ranges of each fossil ostracod species are rounded to the nearest 1 Myr. For each stage, the ostracod data displayed are those occurrences whose ranges started either before or during the stage and ended either after or during it.

3.5 | Paleoclimate Reconstructions

To assess the paleoclimate regime relevant to the ostracod distributional patterns, we used climatic simulations conducted using the general circulation model (GCM) FOAM (Jacob 1997), a mixed-resolution ocean–atmosphere GCM. Pertinent to our study, FOAM has a three-dimensional ocean component comprising 24 unevenly spaced depth levels (Jacob 1997), allowing vertical

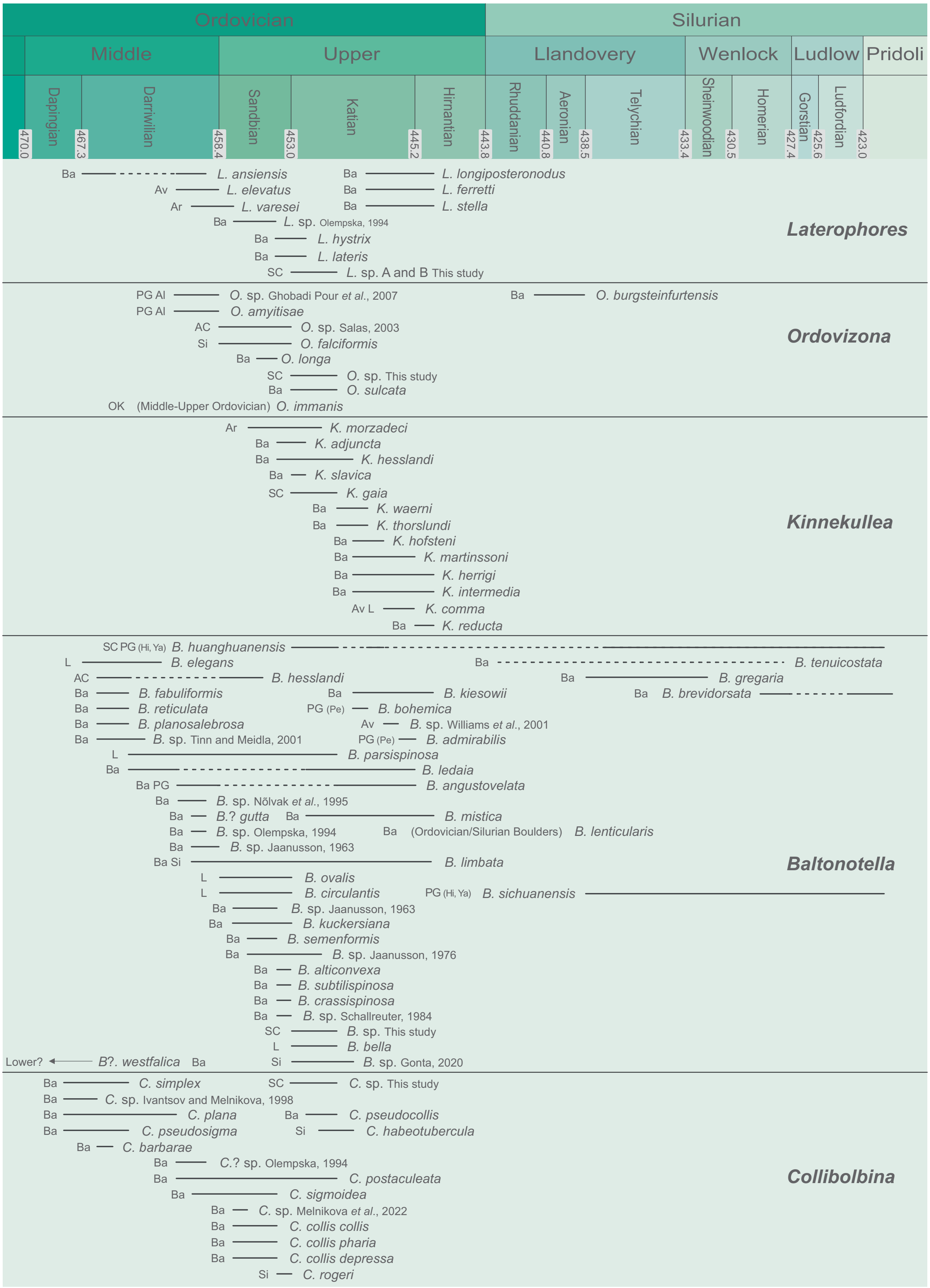

FIGURE 5 | Stratigraphic ranges of all species of the cosmopolitan genera of the Phu Ngu Formation. Initials indicate the paleocontinent each species was found on; Ba = Baltica; Av = Avalonia; Ar = Armorica; SC = South China; OK = Orphan Knoll (Laurentia); Al = Alborz; Si = Siberia; AC = Argentine Precordillera; L = Laurentia; G = Gondwana; PG = Peri-Gondwana; (Pe) = Perunica; (Hi) = Himalaya terrane; (Ya) = Yangtze Platform (South China paleoplate). For full references, see the main reference list. Ages on timescale are after Cohen et al. (2013).

TABLE 1 | Summary of Ordovician species distribution for the ostracod genera *Kinnekullea*, *Laterophores*, *Ordovizona*, *Collibolbina*, and *Baltonotella*. Each number refers to a record of a particular species in the relevant formation—see Table S1 for full list.

Genus	Water depth	Paleogeography	International Time Series and Stage	Formation(s)	Setting	Temperature regime of waters
Baltonotella [1–80]	Shallow (above storm wave base)	Laurentia Tropical to equatorial (< 20°S)	Middle-Upper Ordovician (Darriwilian-Sandbian)	Sunblood Formation [4], Lincolnshire Formation [8], Day Point Formation [10], Valcour Formation [12], Hatter Formation [13], Bromide Formation [15[a] Pooleville Member, 18 Mountain Lake Member], Lexington Limestone—Clays Ferry Formation [16], Oil Creek Formation [19]	Shallow marine—e.g., infralittoral [16], subtidal [15, 19]	Warm surface tropical waters
		Baltica Darriwilian: Subtropical ~35°S Katian: Tropical 20°–30°S	Middle-Upper Ordovician (Darriwilian-Katian); Silurian (Homerian—Pridoli)	Adila Formation [30, 59], Moe Formation [33, 45, 55], Chasmops Shale—Semsvannet locality [75], Furudal Limestone [79], Korgessare Formation [31, 43, 56], Halliku Formation [26, 37, 62]	Shallow marine, onshore [30, 33, 45, 55, 59, 79]; shallow shelf mixed facies [26, 31, 37, 43, 56, 62]	Warm surface tropical waters
		Peri-Gondwana Subtropical ~35°S to high latitude ~60°S	Middle-Upper Ordovician (Darriwilian-Katian)	Domusnovas Formation [34], Shirgesht Formation [35], Králův Dvůr Formation (Perník Bed interval) [64], Bohdalec Formation [71]	Shallow marine—wave-influenced [35, 64, 71]; littoral shoreface [34]	Warm surface tropical waters; Cool polar waters [34, 64, 71]
		Argentine Precordillera Tropical ~30°S	Middle Ordovician (Darriwilian)	Los Azules Formation [65]	Shallow marine	Warm surface tropical waters
	Mid-depth (below storm wave base, relatively proximal)	Laurentia Tropical ~20°S	Upper Ordovician (Sandbian)	Lincolnshire Formation [8], Bromide Formation [15[a]; Pooleville and Mountain Lake Members], Liskeard Formation [2, 47]	Offshore, marine shelf	Warm surface tropical waters, with possibility of cooler deep water influence
		Baltica Tropical 20°–30°S	Upper Ordovician (Katian)	Lower Chasmops Limestone [21], Paekna Formation [40], Boda/*Leptaena* Limestone [67], Ragavere Formation [24, 36, 57], Jonstorp Formation [25, 39, 53]	Below wave base [67]; mud-supported—distal [40]; low in photic zone, mid-shelf [25, 29, 53]; mid-shelf [24, 26, 57]	Warm surface tropical waters, with possibility of cooler deep water influence

(Continues)

TABLE 1 | (Continued)

Genus	Water depth	Paleogeography	International Time Series and Stage	Formation(s)	Setting	Temperature regime of waters
		Avalonia Subtropical ~35°S	Upper Ordovician (Katian)	Cautley Mudstone [77]	Open marine shelf	Warm surface waters, with possible seasonal thermocline influence
		South China Equatorial < 10°N/S	Upper Ordovician (Katian)	Linxiang Formation [72]	Open carbonate platform	Warm surface tropical waters
	Deep (deep/distal shelf, slope)	South China Equatorial < 10°S	Upper Ordovician (Katian)	Phu Ngu Formation [1], Pagoda Formation [73]	Below storm wave base, distal shelf, open marine influence	Influenced by cooler subsurface waters
		Laurentia Tropical-equatorial (< 15°N–20°S)	Upper Ordovician (Sandbian-Katian)	Esbataottine Formation [3], Ardwell Farm Formation [6], Edinburg Formation [7, 17], Bromide Formation [9, 15[a]; Pooleville and Mountain Lake Members], Decorah Shale [14]	Open marine shelf [9, 14, 15]; deeper facies [3, 6, 7, 17]	Influenced by cooler subsurface waters
		Baltica Midlatitude (Darriwilian) ~40°S to tropical 20°–30°S (Katian)	Middle-Upper Ordovician (Darriwilian-Katian)	Montu Formation [23, 63], Saunja Formation [27, 41], Fjäcka Formation [28, 46, 54], Tudulinna Formation [32, 38, 51], Mójcza Limestone [48, 80], Jelgava Formation [52], Holen Limestone [76], Oostriku Formation [42, 58], Hessland Strata G and RII [68–70]	Generally deeper, open marine shelf; deeper part of paleobasin [76]; cold-water carbonate platform, deeper [48, 80]; deep shelf, upper aphotic zone [68–70]; offshore [42, 58]	Cool temperate waters possibly with seasonal thermocline
		Siberia Equatorial < 10°N/S	Upper Ordovician (Sandbian-Katian)	Vessenn'aya Formation [49], Delingde Formation [50]	Deeper marine, cool waters	Influenced by cooler subsurface waters
		Argentine Precordillera Subtropical ~35°S	Upper Ordovician (Sandbian)	Las Aguaditas Formation [66]	Slope	Cooler deep water influence

(Continues)

TABLE 1 | (Continued)

Genus	Water depth	Paleogeography	International Time Series and Stage	Formation(s)	Setting	Temperature regime of waters
Laterophores [81–91]	Mid-depth (below storm wave base, relatively proximal)	Baltica Tropical ~30°S	Upper Ordovician (Katian)	Skagen Limestone [83, 85]	Below wave base	Warm surface waters, with possibility of cooler deep water influence
		Avalonia Midlatitude ~45°S	Middle Ordovician (Darriwilian)	Rorrington Formation [90]	Shelf	Cool temperate waters possibly with seasonal thermocline
	Deep (deep/distal shelf, slope)	South China Equatorial < 10°S	Upper Ordovician (Katian)	Phu Ngu Formation [81, 82]	Below storm wave base, distal shelf, open marine influence	Influenced by cooler subsurface waters
		Armorica High latitude > 60°S	Middle-Upper Ordovician (Darriwilian-Sandbian)	Andouille Formation [84]	Middle offshore, black shales indicate deeper periods (transgression)	Cool surface waters
		Baltica Midlatitude ~35°–40°S	Middle Ordovician (Darriwilian)	Lanna Limestones [86], Komstad Limestone [87], Mójcza Limestone [88, 89, 91]	Deeper part of paleobasin [87]; cold-water carbonate platform, deeper [88, 89, 91]; aphotic zone [86]	Cool temperate waters possibly with seasonal thermocline
Ordovizona [92–101]	Shallow (above storm wave base)	Baltica Tropical ~30° S	Upper Ordovician (Katian)	Hirmuse Formation [93]	Shallow epicontinental sea	Warm surface tropical waters
		Peri-Gondwana and Alborz Subtropical—midlatitude ~30°–40°S	Middle Ordovician (upper Darriwilian)	Shirgesht Formation [97]; Lashkarak Formation [98, 100]	Wave-influenced	Warm surface tropical waters [98] and warm temperate waters [99] possibly with seasonal thermocline
	Mid-depth (below storm wave base, relatively proximal)	Baltica Tropical ~30°S	Upper Ordovician (Katian)	Ragavere Formation [95]	Mid shelf	Warm surface tropical waters, with possibility of cooler deep water influence

(Continues)

TABLE 1 | (Continued)

Genus	Water depth	Paleogeography	International Time Series and Stage	Formation(s)	Setting	Temperature regime of waters
	Deep (deep/distal shelf, slope)	South China Equatorial < 10°S	Upper Ordovician (Katian)	Phu Ngu Formation [92]	Below storm wave base, distal shelf, open marine influence	Influenced by cooler subsurface waters
		Baltica Tropical ~30°S	Upper Ordovician (Katian)	Saunja Formation [94], Montu Formation [96]	Deeper, basinward shelf	Warm tropical waters, with possibility of cooler deep water influence
		Siberia Equatorial < 10°N/S	Upper Ordovician (Sandbian)	Vesenn'aya Formation [99]	Deeper marine, cool waters	Influenced by cooler subsurface waters
		Argentine Precordillera Tropical ~30°S	Upper Ordovician (Sandbian)	Las Aguaditas Formation [101]	Slope	Probably influenced by cooler subsurface waters
Kinnekullea [102–119]	Shallow (above storm wave base)	Baltica Tropical ~30°S	Upper Ordovician (Katian)	Halliku Formation [108]	Shallow shelf, mixed facies	Warm surface tropical waters
	Mid-depth (below storm wave base, relatively proximal)	Baltica Tropical ~30°S	Upper Ordovician (Katian)	Jonstorp Formation [103, 109, 114, 116], Kuldiga Formation [107, 117, 118]	Low in photic zone (mid-shelf) [103, 109, 114, 116]; open or mid-shelf [107, 117, 118]	Warm surface tropical waters, with possibility of cooler deep water influence
	Deep (deep/distal shelf, slope)	South China Equatorial < 10°S	Upper Ordovician (Katian)	Phu Ngu Formation [102]	Below storm wave base, distal shelf, open marine influence	Influenced by cooler subsurface waters
		Baltica Tropical ~20°–30°S	Upper Ordovician (Sandbian-Hirnantian)	Fjäcka Shale [104, 113, 115], Mossen Formation [111], Saunja Formation [112]	Open shelf, deeper part of the basin	Warm surface tropical waters, with possibility of cooler deep water influence
		Laurentia Tropical ~20°S	Upper Ordovician (Katian)	Lady Burn and South Threave Formations [105]	Forearc basin	Cooler deep water influence
		Avalonia Subtropical ~35°S	Upper Ordovician (Katian)	Cautley Mudstone Formation [106]	Deeper marine shelf	Warm waters with possible seasonal thermocline influence

(Continues)

TABLE 1 | (Continued)

Genus	Water depth	Paleogeography	International Time Series and Stage	Formation(s)	Setting	Temperature regime of waters
		Armorica Terrane High latitude > 60°S	Upper Ordovician (Sandbian-Katian)	La Sangsuriere Formation [110]	Distal shelf	Cool polar waters
Collibolbina [120–137]	Shallow (above storm wave base)	Siberia Equatorial < 10°N/S	Upper Ordovician (Sandbian-Katian)	Mangazeya Formation [121, 122]	Carbonate platform—above storm wave base	Possibly influenced by cooler subsurface waters upwelling
		Baltica Subtropical—midlatitudes ~35°–40°S	Middle Ordovician (Dapingian-Darriwilian)	Volkhov Formation [124, 135], Lynna Formation [125], Obukhovo Formation [126], Simankovo Formation [127, 133], Furudal Limestone [130]	Above storm wave base [124, 125, 126, 127, 133, 135]; nearshore [130]	Cool temperate waters possibly with seasonal thermocline
	Mid-depth (below storm wave base, relatively proximal)	Baltica Tropical ~30°S	Upper Ordovician (Sandbian)	Gryazno Formation [136]	Below wave base	Warm waters with possible seasonal thermocline influence
	Deep (deep/distal shelf, slope)	South China Equatorial < 10°S	Upper Ordovician (Katian)	Phu Ngu Formation [120]	Below storm wave base, distal shelf, open marine influence	Influenced by cooler subsurface waters
		Baltica Tropical-midlatitudes ~30°–45°S	Middle-Upper Ordovician (Darriwilian-Katian)	Komstad Limestone [123, 134], Mójcza Limestone [128, 129, 131, 137], Strata G, R II of Hessland 1949 [132]	Deeper part of paleobasin [123, 134]; cold-water carbonate platform, deeper [128, 129, 131, 137], deep shelf, upper aphotic zone [132]	Cool temperate waters possibly with seasonal thermocline

[a] [15] occurs across a range of sedimentation depths in the Bromide Formation.

resolution of ocean heat distribution. FOAM has a fast turnaround time, allowing for a range of boundary conditions to be simulated on reasonable real-world timescales, making this GCM well-suited to deep-time paleoclimate work (e.g., Maffre et al. 2022; Wong Hearing et al. 2021a), including in the Ordovician (e.g., Ontiveros et al. 2023; Pohl et al. 2014; Saupe et al. 2020).

For our chosen time intervals of interest, we selected simulations providing the best match with data-derived ocean temperature and ice-sheet extent estimates. Most of these simulations were previously published by Ontiveros et al. (2023) and Ontiveros (2023). We ran an additional simulation for 440 Ma using the same setup but a lower atmospheric CO_2 concentration to best capture the climatic conditions of the Hirnantian glacial maximum (Pohl 2024). The atmospheric pCO_2 concentrations were imposed as follows: 24 times preindustrial atmospheric level (PAL; 1 PAL = 280 ppm pCO_2) for the Darriwilian, 12 PAL for the Sandbian, 8 PAL for the Katian and 3 PAL for the Hirnantian (following Ontiveros et al. 2023; Pohl et al. 2016a). As the simulations were produced using the same continental reconstructions as were used to paleo-rotate the ostracod location data (Marcilly et al. 2022; Ontiveros et al. 2023), ostracod paleo-locations can be mapped onto plots of simulated ocean temperature data to explore distribution patterns with respect to ocean temperatures.

In our study, we use simulated mean annual ocean temperatures because there is no predominant annual ecology shared among modern ostracods, such as a common period of dormancy or a tendency to migrate to deeper waters in a common season. Some taxa are known to migrate from deeper subtidal to shallower littoral environments in winter, while others do the opposite (Hull 1997; Ruiz, González-Regalado, and Muñoz 1997). There is also variation in their reproductive cycles, with different species reproducing across all seasons and varying lifespans (Hull 1997).

The sedimentological context of our compiled ostracod occurrences testifies to contrasting paleo-water depths during the time of deposition, ranging from shallow shelf to deep shelf-slope settings (Table S1). To best investigate the environmental conditions in which Ordovician ostracod assemblages lived, we account for these varying paleo-water depths by comparing our fossil occurrences from shallow shelf environments (above storm wave base, within the upper mixed part of the water column), to identify faunas adapted to prevailing sea-surface temperatures, with deeper occurrences from offshore, mid to deeper shelf settings, and deep shelf-slope settings, to assess temperatures at lower levels in the water column where temperature would be expected to be much cooler. Fossil occurrences interpreted as representing intermediate depths (below storm wave base but relatively proximal shelf settings) are compared with temperatures simulated at both sea surface and mid-shelf depths.

4 | Results

4.1 | Ostracod Assemblage of the Phu Ngu Formation

Wong Hearing et al. (2021b) recognized at least three ostracod taxa in the Phu Ngu Formation: *Kinnekullea gaia* (Figure 3A), *Laterophores* sp. (Figure 3B, referred to herein as *Laterophores* sp. A, as we also identify a second *Laterophores* species, sp. B, Figure 3E) and tentatively *Ordovizona* sp. (Figure 3C). At least four additional taxa are recognized among material collected in 2022, including *Baltonotella* sp. (Figure 3G), *Steusloffina*? sp. (Figure 3F), *Collibolbina* sp. (Figure 3H,I), and one taxon which belongs to the family Aechminidae (Figure 3D). *Baltonotella* has also been identified in the original material of Wong Hearing et al. (2021b).

The eight ostracod species recorded from the Phu Ngu Formation are endemic to the South China paleoplate. However, at genus-level, the assemblage contains a mix of both endemic and cosmopolitan taxa. Of particular interest is the occurrence of the widespread genera *Kinnekullea*, *Laterophores*, *Ordovizona*, *Collibolbina*, and *Baltonotella*. The biostratigraphical ranges and paleogeographical context of species assigned to these genera are summarized in detail later in the discussion.

A range of instars (juveniles) are recognized for several ostracod taxa (population structures demonstrated by length/height plots in Supporting Information Document S1), which, in combination with a lack of size sorting, preferred valve orientation, or visible damage to valves, suggests the assemblage represents a thanatocoenosis (life assemblage; following Boomer, Horne, and Slipper 2003), with only minor post-mortem disturbance, possibly due to bioturbation. Low-energy currents along the seafloor may have produced the rare ostracod lag deposits. In contrast, Wong Hearing et al. (2021b) suggested that the fauna may have been transported from shelf to basin, but detailed sedimentological and population structure evidence was not available to those authors.

4.2 | Sedimentology of the Phu Ngu Formation

Thin sections taken from three horizons collected in 2022 reveal a poorly sorted siltstone, with detrital quartz silt grains alongside shelly fragments in a mud matrix (Figure 4C). The thin sections reveal a mottled texture, which in places is accentuated by a stylolite-like fabric (cf. Gabbott, Zalasiewicz, and Collins 2008; Powell 2003). Pyrite is irregularly dispersed through the sections, and large, dark lenses reveal pyrite framboids 3–51 μm in diameter (Figure 4A). Framboids are found associated with a fragment of shell, possibly ostracod, on at least one occasion (Figure 4F). There are no sedimentary structures observed, either at macro-scale in the field or on a fine-scale in thin section, such as cross-lamination, or ripples, that would be suggestive of current action. There is no evidence for either reverse or normal grading of grain size, which in repeated sequence may have suggested frequent turbidity current deposition. The deposits are predominantly composed of fine clay minerals, with slightly coarser silt-size quartz grains interspersed (Figure 4A,B,E). Any planar fabric that is present is defined by dark lenses (Figure 4E), which are wavy and discontinuous, possibly representing flattened burrows, rather than depositional lamination.

Ostracod valves are dispersed throughout the sediment (Figure 4C), mostly disarticulated; all are decalcified. There is no preferred orientation to the valves. Additionally, lenticular structures composed of well-sorted fine quartz grains and clay minerals, bound by a cryptocrystalline silica cement (Figure 4B,D), reminiscent of structures found in Upper Ordovician and Silurian (and later) black shales and claystones, are interpreted to be agglutinating benthic foraminifera (e.g., Milliken et al. 2007; Schieber 2009; Trela 2016). The mottled texture, along with simple burrow traces observed in the field, indicates that on a fine scale, bioturbation has likely overprinted primary sedimentary structures. However, bedding planes visible in the field suggest this bioturbation was either not deeply-penetrating, or the sedimentation rate was too high for the larger-scale sedimentary structures to be lost.

4.3 | Temporal, Geographical, and Environmental Considerations of the Ostracods

Here, we summarize the temporal, paleoenvironmental, and paleogeographical distribution of all species assigned to those genera in the Phu Ngu Formation that are cosmopolitan (Table 1; Table S1).

The earliest reported *Kinnekullea* is in the Late Ordovician of Armorica (Vannier 1986). The genus ranges from the Sandbian to the Hirnantian, some ~14 Myr (Figure 5). Most *Kinnekullea* species are known from Baltica (e.g., Floyd, Williams, and Rushton 1999; Sidaravičiene 1992; Vannier 1986; Vannier, Siveter, and Schallreuter 1989), except, *K. morzadeci*, from Armorica (Vannier 1986), *K. comma* from Avalonia and Laurentia (Floyd, Williams, and Rushton 1999; Williams et al. 2000, 2001), and *K. gaia* from South China (Wong Hearing et al. 2021b). *Kinnekullea* species occur in carbonate and clastic settings and span tropical to high paleolatitudes (Table 1).

The earliest *Laterophores* is from the Darriwilian of Baltica and Avalonia (Figure 5); species of the genus persist to the Hirnantian, ~23 Myr later (Figure 5). Although predominantly known from Baltica (e.g., Gailite 1971; Schallreuter 1968, 1972, 1986; Schallreuter and Hinz-Schallreuter 2011; Vannier, Siveter, and Schallreuter 1989), *Laterophores* species are also reported from Avalonia (Jones 1987), Armorica (Vannier 1986) and the South China paleoplate (Wong Hearing et al. 2021b). Species of *Laterophores* occur from tropical to high (> 60°S) paleolatitudes and in clastic and carbonate deposits.

Ordovizona is a geographically and chronologically widespread genus (Figure 5), possibly ranging from the Darriwilian (Middle Ordovician) to the early Silurian, spanning ~30 Myr. Species are known from the Argentine Precordillera (unnamed species of Salas 2003), Peri-Gondwana (Ghobadi Pour et al. 2006), Siberia (Melnikova 2000), Baltica (Schallreuter 1969, 1983), and the South China paleoplate (Wong Hearing et al. 2021b). *Ordovizona* species are found in clastic and carbonate lithologies from equatorial to mid-paleolatitudes (< 45°S).

The distinction between the genera *Baltonotella* and *Brevidorsa* remains controversial (Schallreuter and Hinz-Schallreuter 2010a; Sidaravičiene 1992). Here, *Brevidorsa* is regarded as a synonym of *Baltonotella*, following Meidla (1996), as they are difficult to distinguish (Zhang 2023). It is a long-ranging genus (Figure 5), from the Middle Ordovician (Dapingian, possibly earlier) to the late Silurian (Pridoli), some ~50 Myr. *Baltonotella* species are predominantly known from Laurentia and Baltica (e.g., Gatovsky and Vilesov 2022; Harris 1957; Hessland 1949; Meidla 1996, 2014; Melnikova 2000, 2019; Mohibullah, Williams, and Zalasiewicz 2014; Olempska 1994; Rinkevičiūtė et al. 2022; Sarv 1959; Schallreuter 1997, 2000; Schallreuter and Hinz-Schallreuter 2011; Sidaravičiene 1992; Williams and Vannier 1995). Species also occur in Peri-Gondwana (e.g., Lajblova and Kraft 2018; Sun 1988; Wang 2015), the Argentine Precordillera (Salas 2003), Siberia (Gonta 2020), Avalonia (Williams et al. 2001) and the South China paleoplate (herein; Sun 1988; Zhang, Yuan, and Feng 2018). *Baltonotella* species occur in clastic and carbonate lithofacies from tropical to high (~60°S) paleolatitudes.

Collibolbina ranges from the Middle (Dapingian) to the Late Ordovician (Katian), spanning ~20 Myr (Figure 5), and is predominantly known from Baltica (Hessland 1949; Ivantsov and Melnikova 1998, 2003; Krause 1892; Meidla and Tinn 2005; Neckaja 1953; Olempska 1994; Schallreuter 1964, 1969, 1987, 1994; Schallreuter and Hinz-Schallreuter 2013; Sidaravičiene 1992). Baltic species range from the Dapingian to the Katian. Late Ordovician *Collibolbina* species are also known from Siberia (Abushik and Evdokimova 1999; Gonta 2020; Gonta and Kanygin 2018; Ivanova and Melnikova 1977). The Phu Ngu Formation hosts the first *Collibolbina* outside Baltica or Siberia. *Collibolbina* is predominantly found in carbonate deposits, but is also reported from siliciclastic rocks, including the Phu Ngu Formation. It spans equatorial/tropical paleolatitudes in the Late Ordovician of Siberia, South China, and Baltica, and midlatitudes (~40°S) of Baltica in the Middle Ordovician.

The remaining ostracod genera of the Phu Ngu Formation appear endemic to South China. Of these, the possible metacopid *Steusloffina*? sp. is the only species described from elsewhere on the South China paleoplate, in the Huadan Formation (Zhang 2023), Yunnan Province, and the Pagoda Formation (Zhang, Yuan, and Feng 2018), Hubei Province, China. The genus cannot be properly diagnosed without assessing the hinge and valve overlap characteristics, which are not observed in the Chinese or Vietnamese specimens. An undescribed new genus from the Phu Ngu Formation (Figure 3D) belongs to the family Aechminidae, which also suggests a Baltic (Tinn and Meidla 2004) and Laurentian (Williams et al. 2003b) affinity.

Aside from *Steusloffina*? sp., the Phu Ngu assemblage has no species-level similarity with the Pagoda Formation of Hubei Province (Zhang, Yuan, and Feng 2018) and the Huadan Formation of Yunnan Province (Zhang 2023), China. Nevertheless, those ostracod assemblages also include genera with paleobiogeographical links to Baltica, including *Uhakiella*, *Ahlintella*, and *Longiscula* in the Huadan Formation (Zhang 2023). The Huadan Formation represents a mixed siliciclastic-carbonate succession deposited in a nearshore environment, with the ostracods mainly reported from the limestones (Zhang 2023). The Pagoda Formation comprises nodular limestone deposited in a deep, quiet water setting, and has the genus *Baltonotella* in common with Baltica and Laurentia, as well as the Phu Ngu Formation (Zhang, Yuan, and Feng 2018). The Phu Ngu Formation differs from these formations in its siliciclastic lithology and paleo-arc setting. However, it may have formed at similar paleo-depths to the Pagoda Formation.

4.4 | Paleoclimatic Context of Fossil Data Occurrences

For each interval, we plotted the zonal average temperature-depth profiles across all model grid cell latitudes to understand the simulated ocean thermal structure, including the depth range of any thermocline (Figure 6). The profiles show that for most latitudes and time periods the temperature begins to decrease from at least 200 m depth, and starts to homogenize between ~250 and 500 m at mid and high latitudes, and between 500 and 1000 m at low latitudes. For the Darriwilian, the temperature appears to stabilize at ~15°C, for the Sandbian and Katian at ~10°C, and ~0°C for the Hirnantian (Figure 6). Like today, Ordovician oceans were characterized by a thermocline separating a warm upper ocean typified by a strong vertical temperature gradient, and a deeper ocean that was thermally very uniform (Figure 6). Based on our general circulation model simulations, our deepest ostracod occurrences, documented below storm wave base in distal shelf to slope settings, would have been located below, or within, the Ordovician thermocline (see Table S1).

5 | Discussion

Ostracods have traditionally been used as paleogeographical indicators for the Ordovician (e.g., Schallreuter and Siveter 1985), based on their supposedly limited dispersal capability. However, the cosmopolitan range of some of the genera found in the Phu Ngu Formation raises questions about the patterns of migration of the ostracod species therein, notably whether some of these taxa represent evidence for species that had adapted to a psychrosphere and could therefore disperse more easily through the deep ocean. Below, we establish the paleoenvironmental setting of the Phu Ngu Formation, then test the possibility of a paleopsychrospheric ostracod fauna by considering a range of possible alternative explanations for the cosmopolitan range of its taxa, before considering a paleopsychrospheric scenario in more detail using paleoclimatic and paleoceanographic reconstructions.

5.1 | Paleoenvironmental Setting of the Phu Ngu Formation

The general absence of wave or ripple lamination in the Phu Ngu Formation, and the presence of a mixed pelagic and benthic marine assemblage is suggestive of an offshore shelf or slope setting, below storm wave base, and consistent with the paleoarc setting (Tong et al. 2013; Tong and Vu 2011). Graptolites, including *Dicellograptus*, suggest a setting with oceanic influences (e.g., Williams et al. 2003a). Similar mixed graptolite and shelly assemblages that include ostracods have been reported from a deep slope setting in the arc-related geotectonic setting of the Ordovician of the Girvan area, Scotland (e.g., Floyd, Williams, and Rushton 1999). Ash layers in the Phu Ngu Formation are consistent with an arc geotectonic setting for Vietnam during the early Paleozoic (Tong et al. 2013; Tong and Vu 2011). The Phu Ngu Formation ostracod assemblage is dominated by binodicopids, which is consistent with the clastic lithology and a more offshore setting (Vannier, Siveter, and Schallreuter 1989). Globally, repeated oxic-anoxic transitions through the Ordovician have been recorded, including records from Baltica and Laurentia (Page et al. 2007). Sedimentological evidence suggests thermohaline circulation was active from at least the middle Katian (Armstrong and Coe 1997), which would have oxygenated the deep oceans.

Zhang et al. (2022) assessed the redox conditions of intra-shelf basin and slope settings of the Yangtze Sea (South China paleoplate) during the Ordovician. Enrichments of the redox-sensitive metals molybdenum and uranium, and highly reactive iron, indicate the expansion of marine anoxia (and possibly euxinic conditions) onto the Yangtze Platform slope during the Darriwilian, as well as around Baltica and Laurentia (Zhang et al. 2022), through to the middle Katian (Zhang et al. 2011). However, pyrite framboid size distributions and geochemical proxy records (including V_{EF}, U_{EF}, and C_{org}/P ratios) from the middle Yangtze region suggest mainly oxic to dysoxic conditions with only rare anoxic episodes and persistent euxinia not indicated until the middle Katian (Chang et al. 2021). The picture presented from redox-sensitive data is mixed, but likely includes some persistent intervals of dysoxia, anoxia, and potentially euxinia. The sedimentological and paleontological evidence presented here suggests there were some oxic intervals when conditions may have favored deeper-marine ostracod dispersal.

Sedimentological evidence suggests seabed anoxia was either localized or intermittent at the time of deposition of the Phu Ngu Formation. The often poorly defined lamination of the Phu Ngu Formation indicates bioturbation, which is consistent with an oxic seabed. The benthic faunal assemblage, including the ostracods and agglutinating foraminifera, also suggests at least partial oxygenation of the seabed (Schieber 2009).

5.2 | Possible Dispersal Mechanisms of the Ostracods

Here, we consider hypotheses to explain the distribution of the cosmopolitan ostracod genera of the Phu Ngu Formation. First, we address the possibility that the genera represent examples of convergent evolution, and then we discuss the following hypotheses: dispersal of ostracods by surface ocean currents, dispersal via biological agents, pelagic dispersal, and dispersal by island hopping.

5.2.1 | Homeomorphy

It is important to consider whether the taxonomic similarities between the Phu Ngu ostracod assemblage and those of Baltica and Laurentia are examples of convergent evolution between unrelated taxa. Each of the cosmopolitan genera found in the Phu Ngu Formation shares distinct features with other members of their assigned genus. *Baltonotella* sp. (Figure 3G) has the fimbriate marginal structure seen in congeneric species. *Laterophores* sp. A and sp. B are diagnosed by the two nodes of the anterior lobe (Figure 3B,E). *Kinnekullea gaia* possesses the distinctive "embryo-shaped" lobal surface (Figure 3A). *Collibolbina* sp. has distinctive lobal and velar morphology (Figure 3H,I). *Ordovizona* sp. has distinct reticulation in association with a

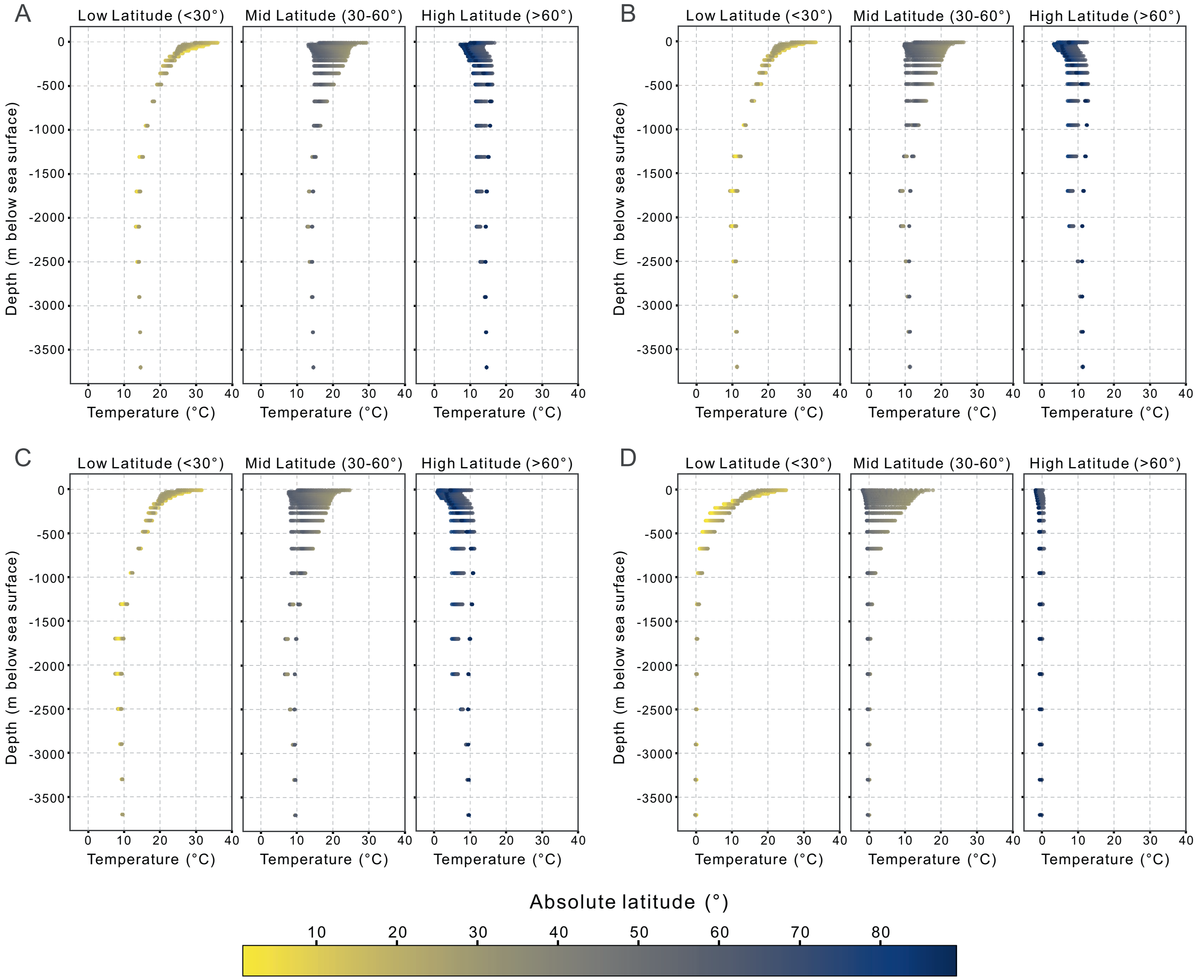

FIGURE 6 | Ocean temperature as a function of water depth in our climatic simulations representative of (A) Darriwilian, (B) Sandbian, (C) Katian, and (D) Hirnantian times. Three latitudinal bands are considered separately for the purpose of analyses: The low latitudes below 30°, the midlatitudes between 30° and 60°, and the high latitudes beyond the polar circle at 60°. Mean-annual, zonally-averaged temperatures are color-coded as a function of latitude. Note the persistence of a thermocline in low and midlatitudes through the Middle and Late Ordovician. Data from Ontiveros (2023) and Pohl (2024).

pit-like sulcus (Figure 3C). These traits, sometimes in combination, are interpreted as shared derived characters unique to each genus, making it unlikely the occurrences in the Phu Ngu Formation are due to convergence.

5.2.2 | Passive Dispersal by Surface Ocean Currents

In some circumstances it may be possible for surface ocean circulation to transport benthic ostracods. A modern example is the Tsushima Warm Current, which transports shelf-living species from the East China Sea to the semi-enclosed marginal southwestern Sea of Japan (Tanaka 2008). Species are also transported from the South China Sea to the East China Sea by the warm Kuroshio Current (Zhao and Wang 1988). However, these modern examples consider transport over comparatively shorter distances (up to 2000 km) with respect to those being discussed here for the Ordovician, which are on the order of ~7000 km, inferred from the relative positions of the Baltica and South China paleocontinents during the Ordovician (e.g., Cocks and Torsvik 2021). Dispersal on the scales we consider for the Ordovician can sporadically occur today, for example, transoceanic transport of ostracods may occur via debris from tsunamis, such as after the 2011 Great East Japan Earthquake (Tanaka, Yasuhara, and Carlton 2018). However, reliance on chance events like tsunamis is not a parsimonious explanation for the consistent, long-term distribution of Ordovician taxa observed.

Linguliform brachiopods from middle-late Katian deposits of Yunnan Province, China, including the ostracod-yielding Pagoda Formation (Zhang 2023), reveal a deep-water micro-brachiopod association with more similarities to Baltica and Avalonia than to the paleogeographically nearer Boshchekul Island Arc (Chen et al. 2022). This pattern resembles that seen for several ostracod genera from the Phu Ngu Formation; for the brachiopods it has been suggested to be a result of possible oceanic circulation patterns, as the Boshchekul Island Arc was in the northern hemisphere during the Katian, while other paleocontinents lay south of the equator (Chen et al. 2022). The South Subpolar Current is thought to have brought cold water to almost equatorial latitudes during the Katian, moving northwards along the western coast of Gondwana and around South China and the Yangtze Platform, lowering the temperatures of surface waters (Jin, Zhan, and Wu 2018; Popov and Cocks 2017). This current was possibly part of a larger gyre that also ran along the Avalonian and Baltican coasts (Pohl et al. 2016b); Chen et al. (2022) ascribe the paleobiogeographical pattern of the linguliforms to this oceanic circulation pattern.

Brachiopod dispersal may be favored by their pelagic larval stage; it is possible that currents could have influenced the distribution of ostracod taxa if some of those were pelagic or had a pelagic larval stage. Prevailing ocean circulation in the tropics is from east to west, so passive dispersal might have enabled migration from continents such as eastern Gondwana and South China westwards to Baltica and Laurentia. However, the ostracod dispersal directions appear either opposite to the pattern expected if reliant on surface ocean currents (e.g., *Collibolbina* originates on Baltica, and appears to migrate eastwards around the equator to Siberia and South China), or seemingly random, suggesting that dispersal by ocean currents is unlikely.

5.2.3 | Pelagic Dispersal

No living podocopes are pelagic or have a pelagic larval stage (Horne 2003); nevertheless, it has been suggested that some fossil podocopes may have been. A functional analysis of some early Paleozoic leiocopid ostracods (e.g., *Baltonotella*) suggested they were poorly suited to be benthic crawlers, and instead may have lived in the water column (Vannier 1990). Other taxa have also been mooted as pelagic, based on their wide paleogeographical distribution, and unusual morphology, notably *Aechmina* (see Siveter 1984; Williams et al. 2001). *Aechmina* species range in age from the Ordovician to Carboniferous. Their most prominent morphological characteristic is an elongate dorsal node, which may have been used as a buoyancy device (e.g., Henningsmoen 1965; Olempska and Chauffe 1999; Siveter 1984; Williams et al. 2001). While *Aechmina* is not part of the Phu Ngu assemblage, *Baltonotella* is. However, *Baltonotella* in the Phu Ngu Formation occurs alongside taxa that may be considered typical benthic forms (*Collibolbina*, *Laterophores*, *Ordovizona*, and *Kinnekullea*), lacking any morphology associated with a pelagic lifestyle, and which are also paleogeographically widespread taxa. A nektobenthic mode of life, which has been suggested for some Ordovician ostracods (e.g., Kanygin 1971; Schallreuter and Hinz-Schallreuter 2010b), would not enable ostracods to cross the wide oceans between the major paleocontinents.

Furthermore, it is notable that the Phu Ngu Formation contains no ostracod species in common with geographically remote Ordovician paleocontinents. Thus, a series of intermediate migratory species is envisaged, perhaps facilitated by the long temporal ranges of the genera (Figure 5), with local allopatric speciation responsible for the fossil distribution patterns. This pattern would not be expected for the (more rapid) dispersal of plankton, noted for Silurian pelagic ostracods (Perrier et al. 2019). Therefore, we suggest that dispersal as plankton is not a parsimonious interpretation of the assemblage.

5.2.4 | Dispersal via Biological Agents

Today, there are several biological vectors by which ostracods can be transported (either as eggs or adults), such as rafting by plant debris (e.g., Coimbra and Carreño 2012; Machado, Coimbra, and Carreño 2005; Morais and Coimbra 2019; Rosa, Martens, and Higuti 2023; Teeter 1973); via the guts of larger animals such as fish (e.g., Vinyard 1979), or birds (e.g., Green et al. 2008; Proctor 1964); or by phoretic behavior, for example using amphibians and reptiles (e.g., Lopez et al. 2005). There were fewer potential media that could have aided ostracod dispersals in the Ordovician. Other transporters of ostracods would be restricted to cephalopods and early fish (Schallreuter and Siveter 1985), but these relationships have yet to be observed for the Ordovician. Land plants were in the early stages of their evolution (Rubinstein et al. 2010; Wellman, Osterloff, and Mohiuddin 2003), and would not have provided suitable rafts for long-distance transport. While dismissing intermittent dispersal by biological vectors such as algae may prove difficult, it is unlikely this transport mechanism that relies on chance, and surface ocean currents, would produce the consistent patterns of the multiple cosmopolitan taxa we describe here.

5.2.5 | Dispersal via Island/Continent Hopping

Ostracods are known to travel great distances via both natural and human-influenced pathways, as either eggs, juveniles, or adults. Today, they disperse via "island-hopping" between geographically proximal shelves and landmasses. For example, the Easter Island ostracod distribution has been attributed to periods of low sea level exposing shallow summits and seamounts, along which the ostracods may have progressively moved east from around Pitcairn Island (Whatley and Jones 1999). Clipperton Island in the eastern Pacific is seen as a bidirectional "stepping-stone for migration" across the Eastern Pacific Barrier for ostracods, mollusks, and foraminifera (McGann, Schmieder, and Loncke 2019).

Island hopping has also been attributed to longer-term migration patterns of ostracods, for example, *Kotoracythere inconspicua* spreading across the western Pacific through the Miocene (Witte and van Harten 1991). In deep time, an overall trend of increased ostracod migration when the sea level is low, compared to less migration at times of high sea level, is noted in the Ordovician (Williams et al. 2003b). It has been suggested some early Silurian ostracods migrated via island-hopping routes between the Iranian portion of Gondwana, Baltica, and Laurentia during low sea levels (Hairapetian et al. 2011). Island hopping across shallow shelves has also been attributed to the faunal links between Laurussia and Gondwana though the late Silurian and Devonian (Nazik et al. 2018).

For the Silurian, ostracod paleobiogeographical distribution has been broadly explained by geographical isolation and global sea-level changes (Song et al. 2022). The late Llandovery-Pridoli ostracod fauna of the Pulu Formation (Tethyan Himalaya terrane) is interpreted as a shallow-marine, offshore deposit, and shares affinities with taxa from Laurentia and Baltica, as well as *Baltonotella sichuanensis* and *B.* cf. *huanghuaensis* known from South China (Song et al. 2022). There, faunal exchanges between peri-Gondwana and Baltica were possibly due to sea-level changes (Song et al. 2022); the Tethyan Himalaya terrane was near to the South China paleoplate during the Silurian, and possibly separated by a shallow sea (Song et al. 2022), which may have enabled migration via island hopping. Island hopping principals can also be applied to seamounts (Larwood and Whatley 1993). However, for both seamounts and islands, ostracods that are strongly constrained by temperature or depth would not be able to migrate without the aid of other vectors or changes in sea level.

Based on the current fossil record, island hopping does not explain the long-term migration routes for the taxa we evaluate. Indeed, the dispersal of species of *Baltonotella* between Baltica and Laurentia, and thereafter to South China and Perunica (Figure 5) appears unrelated to geographical proximity and successive translocation of taxa via intermediate connections. Nevertheless, the time factor evident in a reading of Figure 5 may have aided dispersal; *Laterophores*, *Collibolbina*, *Baltonotella*, *Kinnekullea*, and *Ordovizona* are all long-ranging taxa (all > 10 Myr). That these genera persist over timescales of millions of years means that there is a greater chance of species dispersal, via emergent ocean islands, by the juxtaposition of continental shelves, or by changes in sea level. It is important to note that during the early Katian sea level was high (Haq and Schutter 2008; Munnecke et al. 2010), though some records, such as those from Baltoscandia, suggest the highstand occurred later in the mid-Katian (Nielsen 2004). As a dispersal mechanism, island hopping likely would have faced formidable ocean barriers to migration during the interval of the Phu Ngu Formation deposition, given the position of South China relative to Baltica and Laurentia. However, it is possible that the current distribution of assemblages of Ordovician ostracods is very incomplete, and that assemblages from intermediate paleogeographical regions may help to confirm whether island hopping was a possible medium for dispersal.

5.3 | Dispersal of a Psychrospheric Ostracod Fauna

Here, we discuss the possibility that the cosmopolitan genera of the Phu Ngu Formation are indicative of an early psychrosphere, with ostracods that were able to migrate via cooler, deeper waters within and below the thermocline. First, we assess the climatic considerations needed to establish and maintain a psychrosphere, before returning to the ostracod data and discussing its compatibility with a paleopsychrospheric distribution.

5.3.1 | Paleoclimatic and Paleoceanographic Considerations for a Psychrosphere

From the discussion above, it follows that the distribution pattern of the more widespread genera from the Phu Ngu Formation cannot easily be explained by the migration of benthic species along shallow-shelf continental margins or island-hopping during periods of low sea level. However, if species of these genera were able to migrate via cooler, deep water within and below the thermocline then the cooler, deep oceans between the paleocontinents would not have presented such an impenetrable barrier. This section discusses whether the Phu Ngu ostracod fauna suggests an early psychrosphere, whether the ocean and climate state through the Ordovician would have supported the presence of a thermocline, and the physiological implications for a psychrospheric fauna.

As the psychrosphere is formed of cold, deep waters, its presence is influenced by the prevailing climate state, being dictated to an extent by the presence of ice sheets at high latitudes, which may encourage the production of cold bottom waters and the onset of thermohaline circulation (see, e.g., Benson 1975; Corliss 1979; Kennett 1977; Kennett and Shackleton 1976). Before the major Hirnantian glaciation, ice sheets may have been present on Gondwana from the early/middle Katian (Armstrong and Coe 1997; Finnegan et al. 2011; Loi et al. 2010; Pope and Read 1998), or even the Darriwilian (e.g., Herrmann et al. 2004; Pohl et al. 2016a), though of smaller extent compared to the latest Katian/Hirnantian (Kidder and Tomescu 2016). Sedimentological, paleontological, and stable-oxygen-isotope data suggest a transition from warm to cool water conditions by the early Katian of South China (Jin, Zhan, and Wu 2018), a trend also seen in Laurentia (e.g., Brookfield 1988; Lavoie 1995). Therefore, a psychrosphere may have evolved during the Middle Ordovician resulting from global cooling (e.g., Herrmann et al. 2004; Trotter et al. 2008). Such an inference is consistent with climate simulations for the Ordovician oceans, which show a steep thermal gradient of up to 20°C cooling from the surface to ~1000 m depth in the tropics (Figure 6), though noting that the deep-ocean temperatures are much warmer in the Darriwilian (15°C) and the Sandbian and Katian (~10°C) than present (4°C). By comparison, the deep oceans of the Hirnantian appear to be even colder than present, stabilizing at ~0°C.

It is necessary to consider the depositional setting of the Phu Ngu Formation and whether it was deposited within or below the thermocline. In the early Katian (~453 Ma), northeast Vietnam was likely on the eastern edge of the equatorial South China paleoplate, facing Peri-Gondwana (Cocks and Torsvik 2021; Torsvik and Cocks 2013). Servais et al. (2014) suggested hypothetical upwelling zones on the western margins of Laurentia (0°–30°N and°S), and Gondwana (30°–60°S), induced by westerly winds. Upwelling may have occurred further west, around the Yangtze platform and therefore South China (Jin, Zhan, and Wu 2018; Zhang et al. 2022), at least by the late Katian (Yang, Hu, and Wang 2021). Graptolite assemblages along the Vietnamese margin of the South China paleoplate, evident for example in the Phu Ngu Formation, suggest oceanic influences (see, for comparison, Williams et al. 2003a) despite possibly facing away from the open ocean. These factors, and the geotectonic setting (Tong et al. 2013; Tong and Vu 2011), suggest that the environmental setting of the Phu Ngu Formation was influenced by cooler oceanic waters below storm wave base and likely considerably cooler than the local sea-surface temperature.

An additional limitation for an Ordovician ostracod psychrosphere may have been the depth of the lysocline. Accurate estimates for the depth of the carbonate compensation depth (CCD) during the Katian are difficult to constrain, because of the absence of deep-ocean sedimentary deposits and lack of open-ocean calcifiers before the Mesozoic. However, the CCD in the Ordovician was likely shallower than the present, due to a combination of factors, including higher atmospheric pCO_2 (estimates range between 3 and over 15 times PAL; Berner 2006; Pohl et al. 2016a, 2016b); low calcium carbonate saturation in surface waters (Mackenzie and Morse 1992); relatively high sea levels (Haq and Schutter 2008); and cratonic flooding (Algeo and Seslavinsky 1995). Nevertheless, a review of modern ostracod assemblages recovered from as deep as almost 8200 m reveals relatively diverse and/or abundant populations, showing that ostracods can adapt to live successfully below the CCD (Brandão et al. 2019; Brandt et al. 2019). Whether ostracods were able to survive below the CCD in the Ordovician, or whether this is a specialized trait that evolved later is another question. It is possible that the fossil record of ostracods below the CCD is sparse due to the post-mortem dissolution of valves (Brandão et al. 2019) and the rarity of preserved pre-Jurassic deep oceanic sedimentary deposits.

5.3.2 | Paleopsychrospheric Ostracods of the Phu Ngu Formation

The ostracod assemblage of the Phu Ngu Formation contains species of taxa that at the generic level are widely dispersed globally and include those that are cold water-adapted (Table 1, Figures 7–9). We suggest that some of the species of these taxa may have migrated via cooler and deeper ocean water masses, including via a psychrosphere. Here, we examine evidence that the cosmopolitan genera that have species found in the Phu Ngu Formation include deeper-water, cold-adapted species elsewhere. Formations considered to be deep shelf or slope environments were not necessarily deposited within the psychrosphere (i.e., below the thermocline), but would certainly have been within the thermocline (Figure 6), experiencing much cooler temperatures than shallow shelf deposits at a similar latitude.

Kinnekullea species are known from high (La Sangsuriere Formation; Vannier 1986), subtropical, and tropical paleolatitudes (e.g., Cautley Mudstone Formation; Williams et al. 2001; Table 1, Figures 7–9). *Laterophores* is reported from high (Andouille Formation; Vannier 1986), mid (Ffairfach Group; Jones 1987), and tropical paleolatitudes (e.g., this study). Species of both genera are mostly found in deeper shelf settings. Importantly, *Kinnekullea gaia* and *K. comma* appear to have been adaptable to deeper, cooler-water settings in the tropics (Table 1, Figures 8 and 9), as evidenced by their occurrence in the Phu Ngu Formation of Vietnam (*K. gaia*) and the Upper Drummock Group of Scotland (*K. comma*, Floyd, Williams, and Rushton 1999; Williams et al. 2000). One of the two occurrences of *Kinnekullea* in a shallower marine succession (aside from records from glacial erratics of unknown origin suggested to have been deposited in a shallow shelf environment; Schallreuter 1971) is that of *K. comma* in the Portrane Limestone of Ireland (Orr 1987, unpublished thesis), which was deposited on midlatitude Avalonia during the Katian (Ferretti, Bergström, and Sevastopulo 2014), likely in cooler, temperate waters. As it is unpublished, the Portrane Limestone record is not included in our paleogeographic reconstructions but remains pertinent to the discussion. The other shallow *Kinnekullea* record is *K. intermedia* from the Katian-age, shallow shelf deposits of the Halliku Formation, Estonia (Meidla 1996). Overall, the pattern for *Laterophores* and *Kinnekullea* follows that observed by Guitor and Meidla (2022) and Vannier, Siveter, and Schallreuter (1989), in which binodicopes become proportionally more abundant as part of the overall assemblage with distance from the shore, and in more clastic-rich deposits.

Species of the palaeocopid *Ordovizona* appear to be cooler water-adapted (Table 1, Figures 7–9). *Ordovizona* is often reported from the deeper shelf (e.g., Melnikova 2000; Salas 2003), suggesting that species preferred cooler water. When *Ordovizona* is reported from shallower settings, with the exception of the shallow, epicontinental sea deposits of the Hirmuse Formation (Vinn, Wilson, and Toom 2015), it is from temperate regions where possibly they would have been affected by a seasonal thermocline. For example, *Ordovizona amyitisae* reported from the Shirgesht and Lashkarak formations, of Iran, interpreted to be deposited in wave-influenced, shallow marine settings on Peri-Gondwana and the mid-paleolatitude Alborz paleoplate (Bayet-Goll et al. 2016; Ghobadi Pour et al. 2006; Ghobadi Pour, Williams, and Popov 2007; Schallreuter et al. 2006).

Species of the palaeocopid *Collibolbina* are recorded from both shallow and deeper marine settings from subtropical to mid-paleolatitude settings. *Collibolbina* species found in the shallow water tempestite deposits of the Mangazeya Formation of the equatorial Siberian Platform (Gonta and Kanygin 2018; Ivanova and Melnikova 1977), interpreted as cold water carbonate facies resulting from cool waters upwelling at a time of high sea level (Dronov 2013; Dronov et al. 2009), support a possible cold water adaptation.

Species of the leiocopid *Baltonotella* are widely recorded globally (Table 1, Figures 7–9). They often occur in shallow shelf facies from equatorial to high paleolatitudes. For example, *Baltonotella admirabilis* is reported from marginal marine deposits of the Králův Dvůr Formation (Lajblova and Kraft 2018), and *B. bohemica* from the *Cruziana* ichnofacies of the Bohdalec Formation (Mikulas 1994), Czechia, at > 60°S in the Ordovician (Lajblova and Kraft 2018). *Baltonotella angustovelata* occurs in the Shirgesht Formation, east-central Iran, in a shallow marine, wave-influenced paleoenvironment (Bayet-Goll et al. 2016; Ghobadi Pour et al. 2006; Schallreuter et al. 2006) and the Domusnovas Formation, Sardinia, in a littoral shoreface paleoenvironment (Leone et al. 2002; Loi et al. 2023; Schallreuter et al. 2007). These formations were likely forming at mid-paleolatitudes outboard of Gondwana (Loi et al. 2023). The mid-paleolatitude *Baltonotella hesslandi* from the Argentine Precordillera occurs in shelf (Los Azules Formation) and slope (Las Aguaditas Formation) paleo-settings (de García and Proserpio 1978; Salas 2003).

Many *Baltonotella* are from the tropical-subtropical paleolatitudes of Laurentia, where species occur in a wide range of depths, from shallow to deep shelf. *Baltonotella* is recorded from mid to

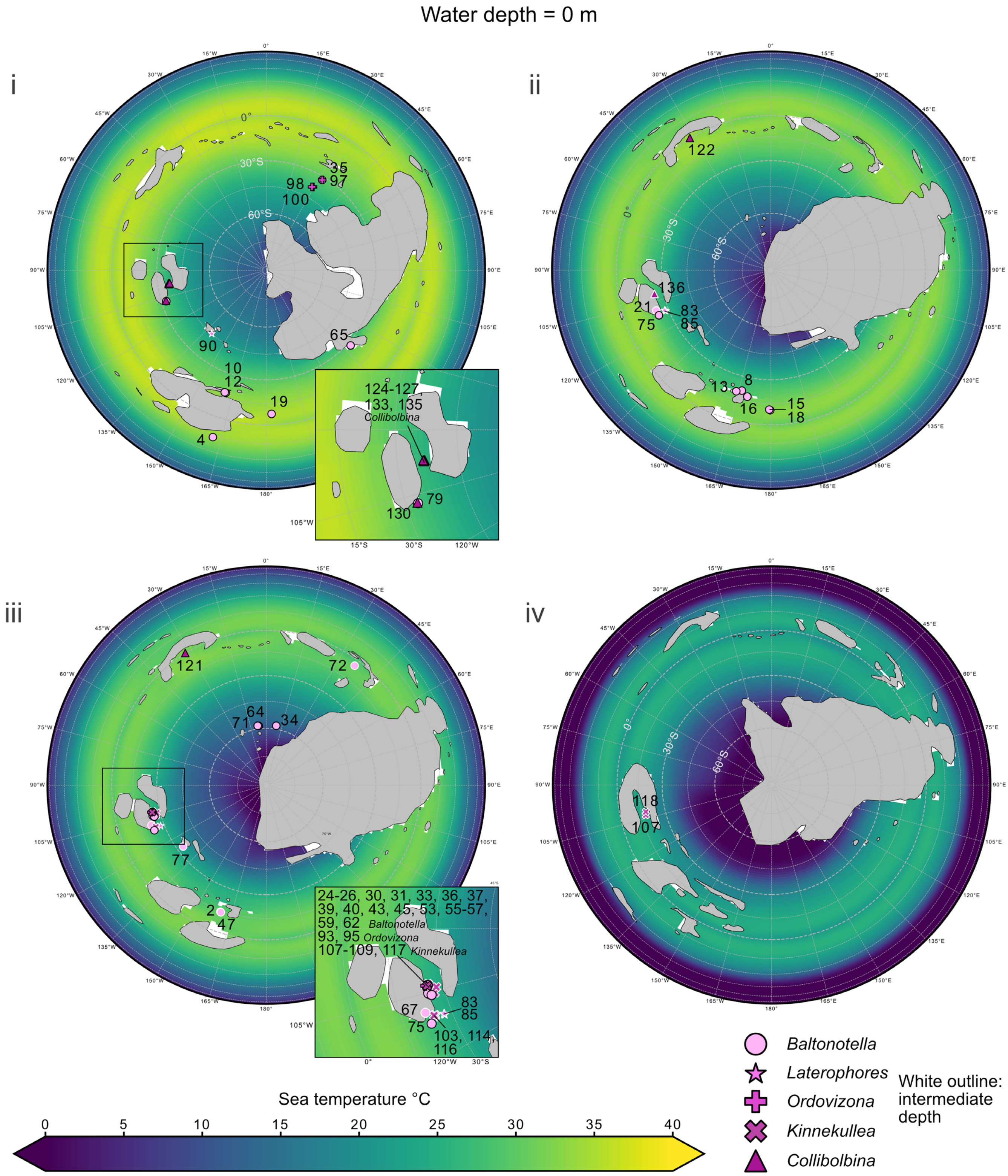

FIGURE 7 | Distribution of ostracods vs. simulated ocean temperatures. Distribution of species of the ostracod genera *Collibolbina*, *Laterophores*, *Ordovizona*, *Baltonotella*, and *Kinnekullea* for Darriwilian (i), Sandbian (ii), Katian (iii), and Hirnantian (iv) shallow marine shelf settings regarded as above storm wave base (black marker outline) and intermediate depths (white outline). Lambert azimuthal equal-area projection, centered on the South Pole. Sea-surface temperature is displayed; exposed land is shaded gray. Note that there are no shallow shelf ostracod occurrences for the Hirnantian (iv). Numbers on each map represent a record of a species in a specific formation—see Table S1.

deep shelf environments at several equatorial localities, including *Baltonotella* cf. *huanghuanensis*, found in the Pagoda Formation, thought to be deposited in cooler, deeper water settings (Zhang, Yuan, and Feng 2018), contemporaneous to the Phu Ngu Formation. Other deeper, equatorial occurrences of *Baltonotella* include the Late Ordovician paleotropical Vesenn'aya Formation

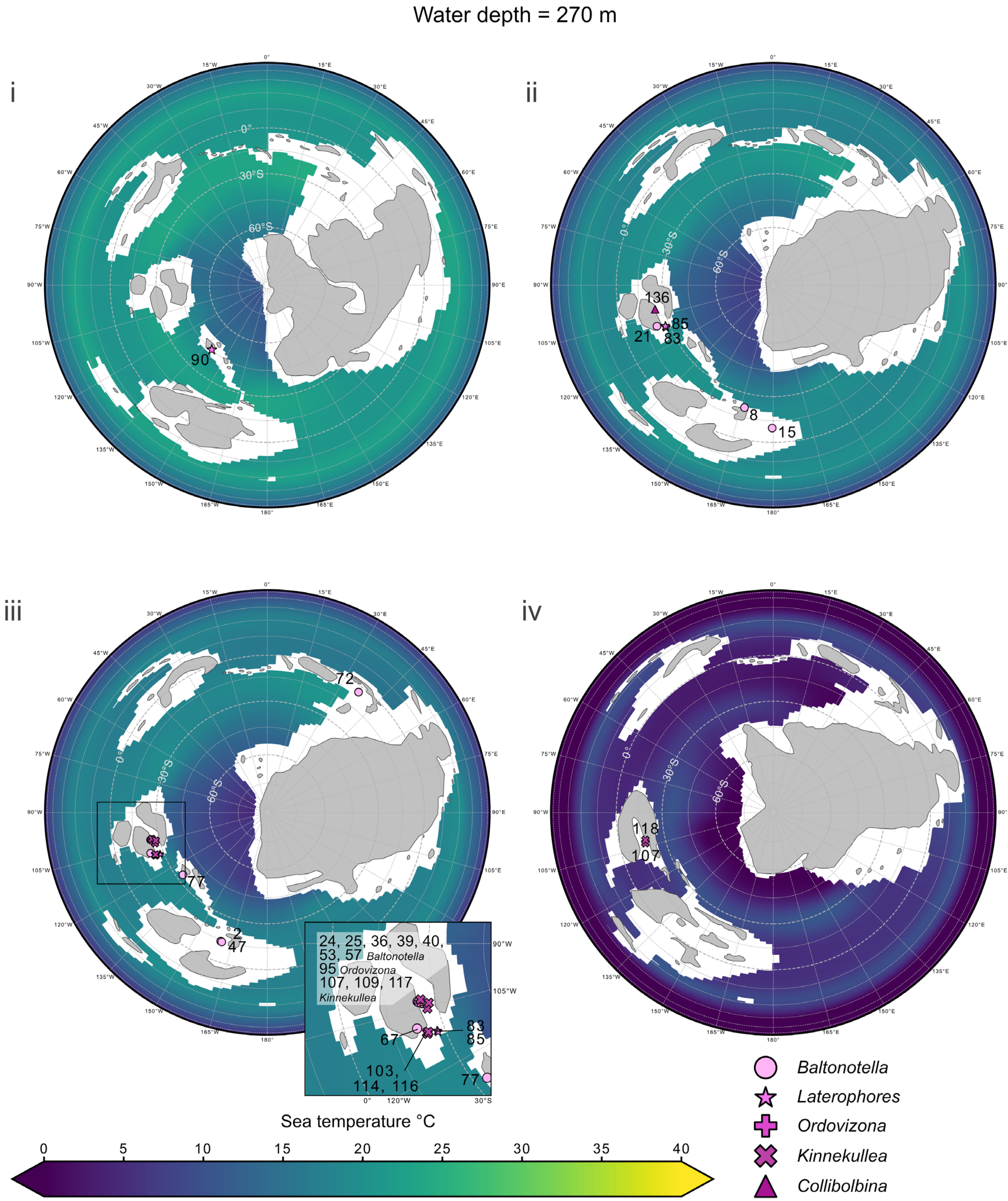

FIGURE 8 | Distribution of ostracods vs. simulated ocean temperatures. Distribution of species of the ostracod genera *Collibolbina*, *Ordovizona*, *Laterophores*, *Baltonotella*, and *Kinnekullea* from intermediate shelf depths for Darriwilian (i), Sandbian (ii), Katian (iii), and Hirnantian (iv). Lambert azimuthal equal-area projection, centered on the South Pole. Ocean temperature for ~270 m water depth is displayed; exposed land is shaded gray, and continental shelves shallower than 270 m are shaded white. Those marine ostracod localities that plot in areas that appear to be land demonstrate uncertainty in defining the paleo-shoreline. Numbers on each map represent a record of a species in a specific formation—see Table S1.

in the Taimyr region of Russia (adjacent to the Siberia paleocontinent during the Late Ordovician, Cocks and Torsvik 2021; Ebbestad and Fortey 2020). The Vesenn'aya Formation includes *Baltonotella limbata* and *Ordovizona falciformis* (Ebbestad and Fortey 2019; Melnikova 2000). Melnikova (2000) suggested the assemblage occupied a cold and deep marine setting and most

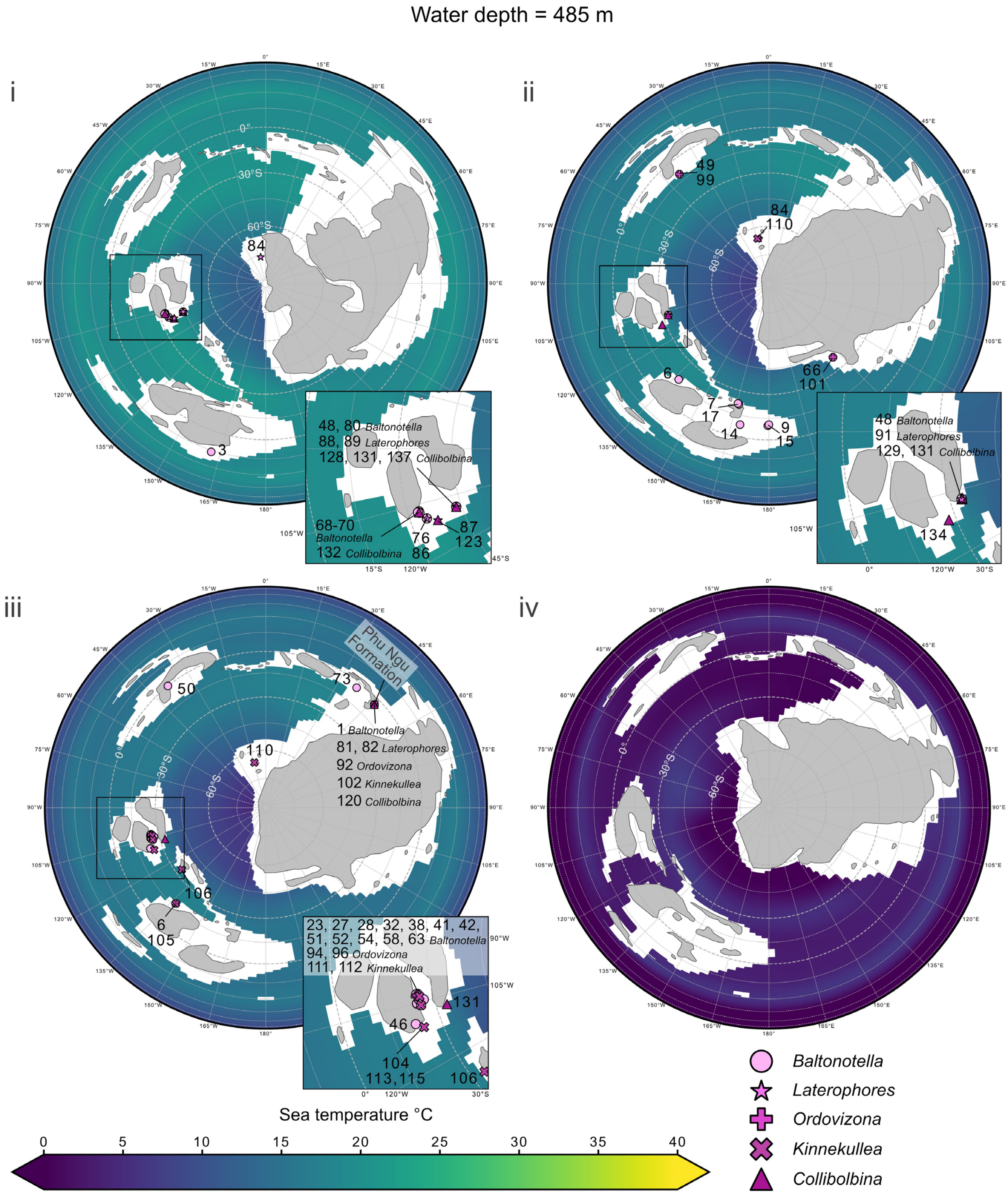

FIGURE 9 | Distribution of ostracods vs. simulated ocean temperatures. Distribution of species of the ostracod genera *Collibolbina*, *Ordovizona*, *Laterophores*, *Baltonotella*, and *Kinnekullea* from deep marine shelf to slope settings for Darriwilian (i), Sandbian (ii), Katian (iii) and Hirnantian (iv). Lambert's azimuthal equal-area projection, centered on the South Pole. Ocean temperature for ~485 m water depth is displayed; exposed land is shaded gray, continental shelves shallower than 485 m are shaded white. Numbers on each map represent a record of a species in a specific formation—see Table S1.

of the ostracods are of the Thuringian Mega-assemblage (*sensu* Bandel and Becker 1975). In Laurentia, the ostracod assemblages of the Late Ordovician (Sandbian) Lower Esbataottine Formation, Mackenzie District, Canada, are also interpreted as preferring a cooler and deeper marine shelf environment (Copeland 1982). One of the species therein, *Baltonotella parsispinosa*, is widespread in deeper shelf facies of the Bromide Formation, Oklahoma (Williams and Siveter 1996), and Edinburg Formation, Virginia, USA (Kraft 1962; Mohibullah et al. 2012). *Baltonotella parsispinosa* is also known from the Late Ordovician paleo-arc setting Ardwell Farm Formation, Scotland, probably transported from a distal shelf/slope setting via turbidity currents (Mohibullah et al. 2011). *Baltonotella* was therefore not uncommon in cooler, deeper waters from tropical and equatorial settings. Thus, while some *Baltonotella* species are shallow marine and warm water, some from tropical/equatorial settings are clearly deeper marine, suggesting cold water adaptation.

Therefore, the occurrence of *Laterophores*, *Ordovizona*, *Kinnekullea*, *Collibolbina*, and *Baltonotella* species in the deeper-marine setting of the Phu Ngu Formation of Vietnam is consistent with the presence of cool water-adapted species of these genera elsewhere, and with the interpretation of an Ordovician ostracod psychrosphere. The relatively homogeneous thermal landscape at deeper water depths (Figure 6) would have facilitated their dispersal over large latitudinal ranges.

6 | Conclusions

The ostracod fauna of the Phu Ngu Formation is dominated by taxa that at the generic level are cosmopolitan, showing links with Laurentia, Baltica, Avalonia, Siberia, the Argentine Precordillera, and Peri-Gondwana (Table 1). There are no clear marine shelf-connections by which species of these benthic taxa could have reached the South China paleoplate, and it is therefore plausible that some of the species migrated via an Ordovician psychrosphere. An Ordovician ostracod psychrosphere is consistent with climate simulations of the Darriwilian, Sandbian, and Katian that show a strong thermal depth gradient and a thermocline in the tropics, shoaling to the surface in mid- to high latitudes, albeit with warmer deep ocean temperatures than at present (Figure 6).

Global analysis shows that *Baltonotella*, *Laterophores*, *Kinnekullea*, *Collibolbina*, and *Ordovizona* include warm and cold water-adapted species, and taxa that are cool- and deep-water adapted in the tropics, such as *Kinnekullea gaia* and *Ordovizona falciformis*. Although it is unlikely that any of the formations we have discussed were deposited within the psychrosphere itself (see Table S1), the overall distribution patterns demonstrate the propensity for cold water adaptation in some Ordovician benthic ostracod taxa that is consistent with the development of a psychrospheric community.

The development of Ordovician ostracod psychrospheric faunas has implications for the resilience of global ostracod faunas to climate change. Long-term survival of the Thuringian Mega-assemblage (Ordovician to Permian; Melnikova 2000) has previously been attributed to a psychrosphere providing a refugia for ostracods across the Late Devonian and Permian–Triassic mass extinctions (Benson 1988; Crasquin and Horne 2018). The time gap between the Thuringian Mega-assemblage going extinct in the Late Triassic, and the establishment of the modern psychrospheric ostracod fauna in the early Cenozoic (Benson 1988) may be due to the warmer climate of the Mesozoic greenhouse leading to deep-ocean anoxia and a decrease in thermohaline circulation (Crasquin and Horne 2018). The success of species within psychrospheric ostracod genera may be a result of their tolerance of a range of depths and temperatures, allowing them to migrate via psychrospheric waters, but also to survive climatic events, such as significant sea-level and temperature changes that would particularly affect shelf faunas. It is notable that species of *Ordovizona* and *Baltonotella* survived the Late Ordovician mass extinction, possibly due to their tolerance of a wide range of marine environments. An ostracod psychrosphere from the Late Ordovician would be consistent with the stratigraphical range of the Thuringian Mega-assemblage (Melnikova 2000). Furthermore, recognizing that such taxa are widespread and decoupling their cosmopolitan biogeographical signal from those that are obligate shallow marine and endemic, is a prerequisite for producing more realistic Paleozoic paleogeographies.

Acknowledgments

We thank Annika Burns for producing sedimentological thin sections; Sarah Gabbott for advice on the sedimentology; Linda Marvin for help with SEM imaging; and Alexander Rutson and Daniel Potts for support with Python (all University of Leicester). Anna McGairy acknowledges a Natural Environment Research Council (NE/S007350/1), Central England NERC Training Alliance PhD studentship. Mark Williams thanks the Leverhulme Trust for supporting the project “The early Palaeozoic evolution of NE Vietnam” (RF-2018-275/4), and Mark Williams, Thomas H. P. Harvey, and Alexandre Pohl thank the Trust for supporting the project “Earth System dynamics at the dawn of the animal-rich biosphere” (RPG-2022-233). Phong Duc Nguyen acknowledges the Vietnamese project “Research of the paleoclimatic and paleoenvironmental conditions for the Cambrian sedimentary rocks at typical geoheritage sites in North Vietnam” (TNMT.2023.562.12) and “Research and investigation of the scientific value of geological heritage in some newly opened or expanded road sections to contribute to the preservation and promotion of the value of Dong Van Karst Plateau UNESCO Global Geopark” (DTCN.HG-04/2023). Toshifumi Komatsu is grateful for Grants-in-Aid for Scientific Research (KAKENHI) from the Japan Society for the Promotion of Science (16K05593, 19K04059). This is a contribution to UNESCO project IGCP 735 “Rocks and the Rise of Ordovician Life” (Rocks ‘n’ ROL). Alexandre Pohl acknowledges the support of the French Agence Nationale de la Recherche (ANR) under reference ANR-22-CE01-0003 (project ECO-BOOST) and of the programme TelluS of the Institut National des Sciences de l'Univers, CNRS (project ROSETTA). We are grateful for the constructive comments of two reviewers.

Conflicts of Interest

The authors declare no conflicts of interest.

References

Abushik, A. F., and I. O. Evdokimova. 1999. “Lagoonal to Normal Marine Late Silurian—Early Devonian Ostracode Assemblages of the Eurasian Arctic.” *Acta Geologica Polonica* 49, no. 2: 133–143.

Ainsaar, L., and T. Meidla. 2001. “Facies and Stratigraphy of the Middle Caradoc Mixed Siliciclastic-Carbonate Sediments in Eastern Baltoscandia.” *Proceedings of the Estonian Academy of Sciences. Geology* 50: 5–23. https://doi.org/10.3176/geol.2001.1.02.

Algeo, T. J., and K. B. Seslavinsky. 1995. “The Paleozoic World: Continental Flooding, Hypsometry, and Sealevel.” *American Journal of Science* 295: 787–822. https://doi.org/10.2475/ajs.295.7.787.

Armstrong, H. A., and A. L. Coe. 1997. "Deep-Sea Sediments Record the Geophysiology of the Late Ordovician Glaciation." *Journal of the Geological Society* 154, no. 6: 929–934. https://doi.org/10.1144/gsjgs.154.6.0929.

Bandel, K., and G. Becker. 1975. "Ostracoden aus paläozoischen pelagischen Kalken der Karnischen Alpen (Silurium bis Unterkarbon)." *Senckenbergiana Lethaea* 56: 1–83.

Bayet-Goll, A., P. M. Myrow, G. F. Aceñolaza, R. Moussavi-Harami, and A. Mahboubi. 2016. "Depositional Controls on the Ichnology of Ordovician Wave-Dominated Marine Facies: New Evidence From the Shirgesht Formation, Central Iran." *Acta Geologica Sinica—English Edition* 90, no. 5: 1572–1597. https://doi.org/10.1111/1755-6724.12803.

Becker, G. 1982. "Ostracoda aus Cephalopoden-Führendem Oberdevon im Kantabrischen Gebirge (N-Spanien). 2. Bairdiacea, Cytheracea und Entomozoacea." *Palaeontographica Abteilung A* 178: 109–182.

Becker, G. 2000. "Progress in Mid Palaeozoic Palaeoceanographical Studies From Ostracoda—From Local to Global Importance (A Review)." *Senckenbergiana Lethaea* 80, no. 2: 555–566. https://doi.org/10.1007/BF03043365.

Becker, G., and M. Bless. 1990. "Biotope Indicative Features in Palaeozoic Ostracods: A Global Phenomenon." In *Ostracoda and Global Events*, edited by R. Whatley and C. Maybury, 421–436. London: Chapman and Hall.

Becker, G., C.-D. Clausen, and K. Leuteritz. 1993. "Verkieselte Ostracoden vom Thüringer Ökotyp aus dem-Grenzbereich Devon/Karbon des Steinbruchs Drewer (Rheinisches-Schiefergebirge)." *Courier Forschungs-Institut Senckenberg* 160: 1–131.

Bennett, C. E. 2008. "A Review of the Carboniferous Colonisation of Non-marine Environments by Ostracods." *Senckenbergiana Lethaea* 88, no. 1: 37–46. https://doi.org/10.1007/BF03043976.

Bennett, C. E., D. J. Siveter, S. J. Davies, et al. 2012. "Ostracods From Freshwater and Brackish Environments of the Carboniferous of the Midland Valley of Scotland: The Early Colonization of Terrestrial Water Bodies." *Geological Magazine* 149, no. 3: 366–396. https://doi.org/10.1017/s0016756811000719.

Benson, R. H. 1975. "The Origin of the Psychrosphere as Recorded in Changes of Deep-Sea Ostracode Assemblages." *Lethaia* 8, no. 1: 69–83. https://doi.org/10.1111/j.1502-3931.1975.tb00919.x.

Benson, R. H. 1988. "Ostracods and Palaeoceanography." In *Ostracoda in the Earth Sciences*, edited by P. de Deckker, J.-P. Colin, and J.-P. Peypouquet, 1–26. Amsterdam: Elsevier.

Berner, R. A. 2006. "GEOCARBSULF: A Combined Model for Phanerozoic Atmospheric O_2 and CO_2." *Geochimica et Cosmochimica Acta* 70, no. 23: 5653–5664. https://doi.org/10.1016/j.gca.2005.11.032.

Boomer, I., D. J. Horne, and I. J. Slipper. 2003. "The Use of Ostracods in Palaeoenvironmental Studies, or What Can You Do With an Ostracod Shell?" *Paleontological Society Papers* 9: 153–180. https://doi.org/10.1017/S1089332600002199.

Brandão, S. N., M. Hoppema, G. M. Kamenev, et al. 2019. "Review of Ostracoda (Crustacea) Living Below the Carbonate Compensation Depth and the Deepest Record of a Calcified Ostracod." *Progress in Oceanography* 178: 102144. https://doi.org/10.1016/j.pocean.2019.102144.

Brandt, A., I. Alalykina, S. Brix, et al. 2019. "Depth Zonation of Northwest Pacific Deep-Sea Macrofauna." *Progress in Oceanography* 176: 102131. https://doi.org/10.1016/j.pocean.2019.102131.

Brookfield, M. E. 1988. "A Mid-Ordovician Temperate Carbonate Shelf-The Black River and Trenton Limestone Groups of Southern Ontario, Canada." *Sedimentary Geology* 60, no. 1: 137–153. https://doi.org/10.1016/0037-0738(88)90115-7.

Bruun, A. F. 1957. "Deep Sea and Abyssal Depths." In *Treatise on Marine Ecology and Paleoecology, Memoirs of the Geological Society of America*, vol. 67, 641–672. New York: Geological Society of America.

Chang, X., M. Hou, A. Woods, et al. 2021. "Late Ordovician Paleoceanographic Change: Sedimentary and Geochemical Evidence From Northwest Tarim and Middle Yangtze Region, China." *Palaeogeography, Palaeoclimatology, Palaeoecology* 562: 110070. https://doi.org/10.1016/j.palaeo.2020.110070.

Chen, D., B. Huang, W.-J. Li, R.-Y. Li, and J.-Y. Rong. 2022. "Late Ordovician (Katian) Linguliform Microbrachiopods From North-Eastern Yunnan, South China." *Papers in Palaeontology* 8, no. 1: e1407. https://doi.org/10.1002/spp2.1407.

Cocks, L. R. M., and T. H. Torsvik. 2013. "The Dynamic Evolution of the Palaeozoic Geography of Eastern Asia." *Earth-Science Reviews* 117: 40–79. https://doi.org/10.1016/j.earscirev.2012.12.001.

Cocks, L. R. M., and T. H. Torsvik. 2021. "Ordovician Palaeogeography and Climate Change." *Gondwana Research* 100: 53–72. https://doi.org/10.1016/j.gr.2020.09.008.

Cohen, K. M., S. C. Finney, P. L. Gibbard, and J.-X. Fan. 2013. "The ICS International Chronostratigraphic Chart." *Episodes* 36: 199–204. https://stratigraphy.org/ICSchart/ChronostratChart2023-09.pdf.

Coimbra, J. C., and A. L. Carreño. 2012. "Richness and Palaeo-Zoogeographical Significance of the Benthic Ostracoda (Crustacea) From the Oceanic Island of Trindade and Rocas Atoll, Brazil." *Revista Brasileira de Paleontologia* 15: 189–202.

Copeland, M. J. 1982. "Bathymetry of Early Middle Ordovician (Chazy) Ostracodes, Lower Esbataottine Formation, District of Mackenzie." *Bulletin. Geological Survey, Canada* 347: 1–39.

Corliss, B. H. 1979. "Response of Deep-Sea Benthonic Foraminifera to Development of the Psychrosphere Near the Eocene/Oligocene Boundary." *Nature* 282, no. 5734: 63–65. https://doi.org/10.1038/282063a0.

Crasquin, S., and D. J. Horne. 2018. "The Palaeopsychrosphere in the Devonian." *Lethaia* 51, no. 4: 547–563. https://doi.org/10.1111/let.12277.

de García, E. R., and C. Proserpio. 1978. "Ostrácodos Ordovícicos de la Precordillera de San Juan (Hoja 18c San José de Jáchal)." *Ameghiniana* 15: 391–405.

Dronov, A. V. 2013. "Late Ordovician Cooling Event: Evidence From the Siberian Craton." *Palaeogeography, Palaeoclimatology, Palaeoecology* 389: 87–95. https://doi.org/10.1016/j.palaeo.2013.05.032.

Dronov, A. V., A. V. Kanygin, A. V. Timokhin, T. Y. Tolmacheva, and T. V. Gonta. 2009. "Correlation of Eustatic and Biotic Events in the Ordovician Paleobasins of the Siberian and Russian Platforms." *Paleontological Journal* 43, no. 11: 1477–1497. https://doi.org/10.1134/S0031030109110124.

Ebbestad, J. O. R., and R. A. Fortey. 2019. "Stratigraphy and Trilobite Biofacies of the Late Ordovician of the Taimyr Peninsula, Arctic Russia." In *Papers From the 6th International Conference on Trilobites and Their Relatives, Fossils and Strata*, edited by A. W. Owen and D. L. Bruton, 35–53. The Lethaia Foundation.

Ebbestad, J. O. R., and R. A. Fortey. 2020. "Late Ordovician Trilobites From the Taimyr Peninsula, Arctic Russia." *Journal of Systematic Palaeontology* 18, no. 1: 1–135. https://doi.org/10.1080/14772019.2019.1601643.

Ferretti, A., S. M. Bergström, and G. D. Sevastopulo. 2014. "Katian Conodonts From the Portrane Limestone: The First Ordovician Conodont Fauna Described From Ireland." *Bollettino della Societa Paleontologica Italiana* 53, no. 2: 105–119.

Finnegan, S., K. Bergmann, J. M. Eiler, et al. 2011. "The Magnitude and Duration of Late Ordovician—Early Silurian Glaciation." *Science* 331, no. 6019: 903–906. http://www.jstor.org/stable/25790349.

Floyd, J. D., M. Williams, and A. Rushton. 1999. "Late Ordovician (Ashgill) Ostracodes From the Drummuck Group, Craighead Inlier, Girvan District, SW Scotland." *Scottish Journal of Geology* 35, no. 1: 15–24. https://doi.org/10.1144/sjg35010015.

Gabbott, S. E., D. J. Siveter, R. J. Aldridge, and J. Theron. 2003. “The Earliest Myodocopes: Ostracodes From the Late Ordovician Soom Shale Lagerstätte of South Africa.” *Lethaia* 36, no. 3: 151–160. https://doi.org/10.1080/00241160310004620.

Gabbott, S. E., J. Zalasiewicz, and D. Collins. 2008. “Sedimentation of the Phyllopod Bed Within the Cambrian Burgess Shale Formation of British Columbia.” *Journal of the Geological Society* 165, no. 1: 307–318. https://doi.org/10.1144/0016-76492007-023.

Gailite, L. 1971. “Ostracods of the Family Bollidae (Boucek) of the Ordovician of Latvia.” In *Palaeontology and Stratigraphy of the Baltic and Byelorussia*, vol. 3, 37–50. Vilnius: Mintis.

Gatovsky, Y. A., and A. P. Vilesov. 2022. “Биостратиграфическая характеристика осадочных комплексов палеозоя Западно-Таймырского потенциально нефтегазоносного района по данным бурения [Biostratigraphic characteristics of paleozoic sedimentary series of the west Taimyr potential oil and gas bearing area according to drilling data].” *Ронефть. Профессионально о нефти. [PRONEFT. Professionally About Oil.]* 7, no. 4: 55–67.

Ghobadi Pour, M., M. Williams, T. Meidla, and L. Popov. 2006. “Ordovician Ostracods From East Central Iran.” *Acta Palaeontologica Polonica* 51: 551.

Ghobadi Pour, M., M. Williams, and L. E. Popov. 2007. “A New Middle Ordovician Arthropod Fauna (Trilobita, Ostracoda, Bradoriida) From the Lashkarak Formation, Eastern Alborz Mountains, Northern Iran.” *GFF* 129, no. 3: 245–254. https://doi.org/10.1080/11035890701293245.

Gonta, T. V. 2020. “Ordovician Ostracods From the Chunya River Basin (A Right Tributary of the Podkamennaya Tunguska River, Siberian Platform).” *Paleontological Journal* 54, no. 1: 34–46. https://doi.org/10.1134/S0031030120010049.

Gonta, T. V., and A. V. Kanygin. 2018. “Ordovician Ostracods From the Core of the Gaindinskaya-3 Reference Borehole (Tunguska Syneclise, Siberian Platform).” *Paleontological Journal* 52, no. 5: 520–534. https://doi.org/10.1134/S0031030118050040.

Green, A. J., K. M. Jenkins, D. Bell, P. J. Morris, and R. T. Kingsford. 2008. “The Potential Role of Waterbirds in Dispersing Invertebrates and Plants in Arid Australia.” *Freshwater Biology* 53, no. 2: 380–392. https://doi.org/10.1111/j.1365-2427.2007.01901.x.

Guitor, S., and T. Meidla. 2022. “Changes in the Morphology of Late Ordovician Ostracods Along the Shelf-To-Basin Transect of the Baltic Palaeobasin.” *Estonian Journal Of Earth Sciences* 71: 157–175. https://doi.org/10.3176/earth.2022.11.

Hairapetian, V., M. Mohibullah, L. J. Tilley, et al. 2011. “Early Silurian Carbonate Platform Ostracods From Iran: A Peri-Gondwanan Fauna With Strong Laurentian Affinities.” *Gondwana Research* 20, no. 2: 645–653. https://doi.org/10.1016/j.gr.2010.12.012.

Haq, B. U., and S. R. Schutter. 2008. “A Chronology of Paleozoic Sea-Level Changes.” *Science* 322, no. 5898: 64–68. https://doi.org/10.1126/science.1161648.

Harris, R. 1957. “Ostracoda From the Simpson Group.” *Bulletin. Oklahoma Geological Survey* 75: 1–333.

Henningsmoen, G. 1965. “On Certain Features of Palaeocope Ostracodes.” *Geologiska Föreningen i Stockholm Förhandlingar* 86, no. 4: 329–394. https://doi.org/10.1080/11035897.1965.9626388.

Herrmann, A. D., B. J. Haupt, M. E. Patzkowsky, D. Seidov, and R. L. Slingerland. 2004. “Response of Late Ordovician Paleoceanography to Changes in Sea Level, Continental Drift, and Atmospheric $p\mathrm{CO}_2$: Potential Causes for Long-Term Cooling and Glaciation.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 210, no. 2: 385–401. https://doi.org/10.1016/j.palaeo.2004.02.034.

Hessland, I. 1949. “Investigations of the Lower Ordovician of the Siljan District, Sweden. I. Lower Ordovician Ostracods of the Siljan District, Sweden.” *Bulletin of the Geological Institute of the University of Uppsala* 33: 97–408.

Horne, D. J. 2003. “Key Events in the Ecological Radiation of the Ostracoda.” *Paleontological Society Papers* 9: 181–202. https://doi.org/10.1017/S1089332600002205.

Hull, S. L. 1997. “Seasonal Changes in Diversity and Abundance of Ostracods on Four Species of Intertidal Algae With Differing Structural Complexity.” *Marine Ecology Progress Series* 161: 71–82. https://www.int-res.com/abstracts/meps/v161/p71-82/.

Isozaki, Y. 2019. “A Visage of Early Paleozoic Japan: Geotectonic and Paleobiogeographical Significance of Greater South China.” *Island Arc* 28, no. 3: e12296. https://doi.org/10.1111/iar.12296.

Ivanova, V. A., and L. M. Melnikova. 1977. “New Finds of Tetradellidae and Hollinidae (Ostracoda) in the Middle and Upper Ordovician of Central Siberia.” *Paleontological Journal* 2: 83–90.

Ivantsov, A., and L. M. Melnikova. 1998. “The Lower Ordovician Volkhov and Kunda Horizons and Characteristics of Trilobites and Ostracodes (The Volkhov River, Leningrad Region).” *Stratigraphy and Geological Correlation* 6, no. 5: 471–487.

Ivantsov, A., and L. M. Melnikova. 2003. “The Azeri, Lasnamägi, and Uhaku Ordovician Regional Stages of the Leningrad Region and Their Trilobite and Ostracode Faunas.” *Stratigraphy and Geological Correlation* 11, no. 4: 24–40.

Jaanusson, V. 1963. “Lower and Middle Viruan (Middle Ordovician) of the Siljan District.” *Bulletin of the Geological Institutions of the University of Uppsala* 42, no. 1/6: 1–41.

Jaanusson, V. 1976. “Faunal Dynamics in the Middle Ordovician (Viruan) of Balto-Scandia.” In *The Ordovician System: Proceedings of a Palaeontological Association Symposium Birmingham*, 301–326. Cardiff: University of Wales Press and National Museum of Wales.

Jacob, R. L. 1997. “Low Frequency Variability in a Simulated Atmosphere-Ocean System.” Unpublished doctoral dissertation, University of Wisconsin-Madison.

Jellinek, T., K. Swanson, and I. Mazzini. 2006. “Is the Cosmopolitan Model Still Valid for Deep-Sea Podocopid Ostracods?” *Senckenbergiana Maritima* 36, no. 1: 29–50. https://doi.org/10.1007/BF03043701.

Jin, J., R. Zhan, and R. Wu. 2018. “Equatorial Cold-Water Tongue in the Late Ordovician.” *Geology* 46, no. 9: 759–762. https://doi.org/10.1130/g45302.1.

Jones, C. R. 1987. “Ordovician (Llandeilo and Caradoc) Beyrichiocope Ostracoda From England and Wales. Part 2.” *Monographs of the Palaeontographical Society* 138: 77–114.

Kanygin, A. V. 1971. “Ordovician Ostracods and Biostratigraphy of the Sette-Daban Ridge.” *Proceedings of the Institute of Geology and Geophysics* 128: 1–109.

Kennett, J. P. 1977. “Cenozoic Evolution of Antarctic Glaciation, the Circum-Antarctic Ocean, and Their Impact on Global Paleoceanography.” *Journal of Geophysical Research (1896–1977)* 82, no. 27: 3843–3860. https://doi.org/10.1029/JC082i027p03843.

Kennett, J. P., and N. J. Shackleton. 1976. “Oxygen Isotopic Evidence for the Development of the Psychrosphere 38 Myr Ago.” *Nature* 260, no. 5551: 513–515. https://doi.org/10.1038/260513a0.

Kidder, D. L., and I. Tomescu. 2016. “Biogenic Chert and the Ordovician Silica Cycle.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 458: 29–38. https://doi.org/10.1016/j.palaeo.2015.10.013.

Kozur, H. W. 1972. “Die Bedeutung triassischer Ostracoden für stratigraphische und paläoökologische Untersuchungen.” *Mitteilungen der Gesellschaft der Geologie-und Bergbaustudenten in Österreich* 21, no. 2: 623–660.

Kozur, H. W. 1991. “Permian Deep-Water Ostracods From Sicily (Italy). Part 2: Biofacial Evaluation and Remarks to the Silurian to Triassic Paleopsychrospheric Ostracods.” *Geologisch-Paläontologische Mitteilungen Innsbruck, Sonderband* 3: 25–38.

Kraft, J. C. 1962. “Morphologic and Systematic Relationships of Some Middle Ordovician Ostracoda.” *Memoir—Geological Society of America* 86: 104. https://doi.org/10.1130/MEM86-p1.

Krause, A. 1892. “Neue Ostrakoden aus märkischen Silurgeschieben.” *Zeitschrift der Deutschen Geologischen Gesellschaft* 44: 383–399.

Lajblova, K., and P. Kraft. 2018. “Middle Katian/Lowermost Hirnantian Ostracods From the Prague Basin (Czech Republic): Diversity Responses to the Climatic Changes.” *Bulletin of Geosciences* 93, no. 2: 205–245.

Larwood, J. G., and R. C. Whatley. 1993. “Tertiary to Recent Evolution of Ostracoda in Isolation on Seamounts.” In *Ostracoda in the Earth and Life Sciences*, edited by K. G. McKenzie and P. J. Jones, 531–549. Rotterdam: A. A. Balkema.

Lavoie, D. 1995. “A Late Ordovician High-Energy Temperate-Water Carbonate Ramp, Southern Quebec, Canada: Implications for Late Ordovician Oceanography.” *Sedimentology* 42, no. 1: 95–116. https://doi.org/10.1111/j.1365-3091.1995.tb01273.x.

Leone, F., A. Ferretti, W. Hammann, A. Loi, G. Pillola, and E. Serpagli. 2002. “A General View on the Post-Sardic Ordovician Sequence From SW Sardinia.” *Rendiconti della Società Paleontologica Italiana* 1: 51–68.

Loi, A., F. Cocco, G. Oggiano, et al. 2023. “The Ordovician of Sardinia (Italy): From the ‘Sardic Phase’ to the End-Ordovician Glaciation, Palaeogeography and Geodynamic Context.” *Geological Society, London, Special Publications* 532, no. 1: 409–431. https://doi.org/10.1144/SP532-2022-121.

Loi, A., J. F. Ghienne, M. P. Dabard, et al. 2010. “The Late Ordovician Glacio-Eustatic Record From a High-Latitude Storm-Dominated Shelf Succession: The Bou Ingarf Section (Anti-Atlas, Southern Morocco).” *Palaeogeography, Palaeoclimatology, Palaeoecology* 296, no. 3: 332–358. https://doi.org/10.1016/j.palaeo.2010.01.018.

Lopez, L. C. S., B. Filizola, I. Deiss, and R. I. Rios. 2005. “Phoretic Behaviour of Bromeliad Annelids (Dero) and Ostracods (Elpidium) Using Frogs and Lizards as Dispersal Vectors.” *Hydrobiologia* 549, no. 1: 15–22. https://doi.org/10.1007/s10750-005-1701-4.

Machado, C. P., J. C. Coimbra, and A. L. Carreño. 2005. “The Ecological and Zoogeographical Significance of the Sub-Recent Ostracoda Off Cabo Frio, Rio de Janeiro State, Brazil.” *Marine Micropaleontology* 55, no. 3: 235–253. https://doi.org/10.1016/j.marmicro.2005.03.002.

Mackenzie, F. T., and J. W. Morse. 1992. “Sedimentary Carbonates Through Phanerozoic Time.” *Geochimica et Cosmochimica Acta* 56, no. 8: 3281–3295. https://doi.org/10.1016/0016-7037(92)90305-3.

Maffre, P., Y. Godderis, A. Pohl, Y. Donnadieu, S. Carretier, and G. L. Hir. 2022. “The Complex Response of Continental Silicate Rock Weathering to the Colonization of the Continents by Vascular Plants in the Devonian.” *American Journal of Science* 322, no. 3: 461–492. https://doi.org/10.2475/03.2022.02.

Marcilly, C. M., P. Maffre, G. Le Hir, et al. 2022. “Understanding the Early Paleozoic Carbon Cycle Balance and Climate Change From Modelling.” *Earth and Planetary Science Letters* 594: 117717. https://doi.org/10.1016/j.epsl.2022.117717.

Marcilly, C. M., T. H. Torsvik, and C. P. Conrad. 2022. “Global Phanerozoic Sea Levels From Paleogeographic Flooding Maps.” *Gondwana Research* 110: 128–142. https://doi.org/10.1016/j.gr.2022.05.011.

Marcilly, C. M., T. H. Torsvik, M. Domeier, and D. L. Royer. 2021. “New Paleogeographic and Degassing Parameters for Long-Term Carbon Cycle Models.” *Gondwana Research* 97: 176–203. https://doi.org/10.1016/j.gr.2021.05.016.

Mather, B. R., R. D. Müller, S. Zahirovic, et al. 2024. “Deep Time Spatio-Temporal Data Analysis Using pyGPlates With PlateTectonicTools and GPlately.” *Geoscience Data Journal* 11, no. 1: 3–10. https://doi.org/10.1002/gdj3.185.

McGairy, A., T. Komatsu, M. Williams, et al. 2021. “Ostracods Had Colonized Estuaries by the Late Silurian.” *Biology Letters* 17, no. 12: 20210403. https://doi.org/10.1098/rsbl.2021.0403.

McGann, M., R. W. Schmieder, and L.-P. Loncke. 2019. “Shallow-Water Foraminifera and Other Microscopic Biota of Clipperton Island, Tropical Eastern Pacific.” *Atoll Research Bulletin* 626: 1–28. https://doi.org/10.5479/si.10329962.v1.

Meidla, T. 1996. “Late Ordovician Ostracodes of Estonia.” *Fossilia Baltica* 2: 1–222.

Meidla, T. 2014. “The Ordovician System in Estonia.” In *4th Annual Meeting of IGCP 591 the Early to Middle Paleozoic Revolution Estonia*, edited by H. Bauert, O. Hints, T. Meidla, and P. Männik. Tallinn, Estonia: Institute of Ecology and Earth Sciences, University of Tartu, Institute of Geology at Tallinn University of Technology Geological Survey of Estonia.

Meidla, T., and O. Tinn. 2005. “Ostracods.” In *The 6th Baltic Stratigraphical Conference, IGCP 503 Meeting August 23–25, 2005, Pre-Conference Excursion ‘Cambrian and Ordovician of St. Petersburg Region’ Field Guidebook*, edited by A. V. Dronov, T. Y. Tolmacheva, E. Raevskaya, and M. Nestell. St. Petersburg, Russia: St. Petersburg State University and Baltic Stratigraphical Association.

Melnikova, L. M. 2000. “Ordovician Ostracodes of the Thuringian Ecotype From Northern Taimyr.” *Paleontological Journal* 34, no. 6: 622–631.

Melnikova, L. M. 2019. “Ostracods From the Delingde Formation (Upper Ordovician) of the Siberian Platform.” *Paleontological Journal* 53, no. 2: 140–154. https://doi.org/10.1134/S0031030119020072.

Melnikova, L. M., G. V. Mirantsev, S. S. Terentiev, and G. A. Anekeeva. 2022. “Ostracods of the Gryazno Formation (Upper Ordovician, Sandbian Stage and Idavere Regional Stage) in the West of Leningrad Region.” *Paleontological Journal* 56, no. 5: 510–525. https://doi.org/10.1134/S0031030122050082.

Mikulas, R. 1994. “New Finds of Trace Fossils From the Bohdalec and Kraluv Dvur Formations (Late Ordovician, Barandian Area, Czech Republic).” *Journal of Geosciences* 39, no. 4: 303–312.

Milliken, K., S.-J. Choh, P. Papazis, and J. Schieber. 2007. “‘Cherty’ Stringers in the Barnett Shale Are Agglutinated Foraminifera.” *Sedimentary Geology* 198, no. 3: 221–232. https://doi.org/10.1016/j.sedgeo.2006.12.012.

Mohibullah, M., T. R. A. Vandenbroucke, M. Williams, et al. 2011. “Late Ordovician (Sandbian) Ostracods From the Ardwell Farm Formation, SW Scotland.” *Scottish Journal of Geology* 47, no. 1: 57–66. https://doi.org/10.1144/0036-9276/01-428.

Mohibullah, M., M. Williams, T. R. A. Vandenbroucke, K. Sabbe, and J. A. Zalasiewicz. 2012. “Marine Ostracod Provinciality in the Late Ordovician of Palaeocontinental Laurentia and Its Environmental and Geographical Expression.” *PLoS One* 7, no. 8: e41682. https://doi.org/10.1371/journal.pone.0041682.

Mohibullah, M., M. Williams, and J. Zalasiewicz. 2014. “Late Ordovician Ostracods of the Girvan District, South-West Scotland.” *Monographs of the Palaeontographical Society* 167, no. 640: 1–40. https://doi.org/10.1080/02693445.2013.11963951.

Morais, A. L. M., and J. C. Coimbra. 2019. “Ostracoda (Crustacea) From the Infralittoral of Santa Catarina State, Southern Brazil.” *Marine Biodiversity* 49, no. 1: 69–82. https://doi.org/10.1007/s12526-017-0755-7.

Munnecke, A., M. Calner, D. A. T. Harper, and T. Servais. 2010. “Ordovician and Silurian Sea–Water Chemistry, Sea Level, and Climate: A Synopsis.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 296, no. 3: 389–413. https://doi.org/10.1016/j.palaeo.2010.08.001.

Nazik, A., H. Groos-Uffenorde, E. Olempska, et al. 2018. “Late Silurian and Devonian Ostracods of the Istanbul Zone (Western Pontides) and the Taurides: Palaeogeographical Implications.” *Palaeobiodiversity and*

Palaeoenvironments 98, no. 4: 593–612. https://doi.org/10.1007/s12549-018-0340-5.

Neckaja, A. I. 1953. "Tetradellidy Ordovika Pribaltiki i Ih Stratigraficheskoe Znachenie (Tetradellids of the Ordovician of the East Baltic and Their Stratigraphic Significance)." *Trudy Vsesoyuznogo Neftyanogo nauchnoissledovatel'skogo Geologorazvedochnogo Instituta (VNIGRI)* 78: 309–383.

Nguyen, V. P. 2002. "Ordovician-Silurian and Lower Devonian Graptolite Bearing Beds From Vietnam." *VNU Journal of Science: Natural Sciences and Technology* 18: 38–50.

Nielsen, A. T. 2004. "10. Ordovician Sea Level Changes: A Baltoscandian Perspective." In *The Great Ordovician Biodiversification Event*, edited by B. D. Webby, F. Paris, M. L. Droser, and I. G. Percival, 84–94. New York Chichester, West Sussex: Columbia University Press.

Nõlvak, J., T. Meidla, and A. Uutela. 1995. "Microfossils in the Ordovician Erratic Boulders From South-Western Finland." *Bulletin of the Geological Society of Finland* 67: 3–26.

Olempska, E. 1994. "Ostracods of the Mójcza Limestone." In *Ordovician Carbonate Platform Ecosystem of the Holy Cross Mountains, Poland*, edited by J. Dzik, E. Olempska, and A. Pisera, vol. 53, 129–212. Warsaw, Poland: Palaeontologia Polonica.

Olempska, E., and K. M. Chauffe. 1999. "Ostracodes of the Maple Mill Shale Formation (Upper Devonian) of Southeastern Iowa, U.S.A." *Micropaleontology* 45, no. 3: 304–318. https://doi.org/10.2307/1486139.

Ontiveros, D. E. 2023. "Impact of Global Climate Cooling on Ordovician Marine Biodiversity." Zenodo. v1.2. https://doi.org/10.5281/zenodo.8307366.

Ontiveros, D. E., G. Beaugrand, B. Lefebvre, C. M. Marcilly, T. Servais, and A. Pohl. 2023. "Impact of Global Climate Cooling on Ordovician Marine Biodiversity." *Nature Communications* 14, no. 1: 6098. https://doi.org/10.1038/s41467-023-41685-w.

Orr, P. J. 1987. "Upper Ordovician Ostracodes From Portrane, Eastern Ireland." Unpublished doctoral dissertation, Queen's University of Belfast.

Page, A. A., J. A. Zalasiewicz, M. Williams, and L. E. Popov. 2007. "Were Transgressive Black Shales a Negative Feedback Modulating Glacioeustasy in the Early Palaeozoic Icehouse?" In *Deep-Time Perspectives on Climate Change: Marrying the Signal From Computer Models and Biological Proxies, Special Publications of the Micropalaeontological Society*, vol. 2, 123–156. Bath: Geological Society Publishing House. https://doi.org/10.1144/TMS002.6.

Perrier, V., D. J. Siveter, M. Williams, and D. Palmer. 2019. "British Silurian Myodocope Ostracods." *Monographs of the Palaeontographical Society* 172, no. 651: 1–64. https://doi.org/10.1080/02693445.2018.1509567.

Perrier, V., J. M. C. Vannier, and D J. Siveter. 2011. "Silurian Bolbozoids and Cypridinids (Myodocopa) From Europe: Pioneer Pelagic Ostracods." *Palaeontology* 54, no. 6: 1361–1391. https://doi.org/10.1111/j.1475-4983.2011.01096.x.

Pohl, A. 2024. "Late Ordovician (440 Ma; Hirnantian) Climatic Simulation Conducted Using the General Circulation Model FOAM." Zenodo, v1. https://doi.org/10.5281/zenodo.10610771.

Pohl, A., Y. Donnadieu, G. Le Hir, J. F. Buoncristiani, and E. Vennin. 2014. "Effect of the Ordovician Paleogeography on the (In)stability of the Climate." *Climate of the Past* 10, no. 6: 2053–2066. https://doi.org/10.5194/cp-10-2053-2014.

Pohl, A., Y. Donnadieu, G. Le Hir, et al. 2016a. "Glacial onset predated Late Ordovician climate cooling." *Paleoceanography* 31, no. 6: 800–821. https://doi.org/10.1002/2016PA002928.

Pohl, A., E. Nardin, T. R. A. Vandenbroucke, and Y. Donnadieu. 2016b. "High Dependence of Ordovician Ocean Surface Circulation on Atmospheric CO_2 Levels." *Palaeogeography, Palaeoclimatology, Palaeoecology* 458: 39–51. https://doi.org/10.1016/j.palaeo.2015.09.036.

Pope, M., and J. F. Read. 1998. "Ordovician Metre-Scale Cycles: Implications for Climate and Eustatic Fluctuations in the Central Appalachians During a Global Greenhouse, Non-glacial to Glacial Transition." *Palaeogeography, Palaeoclimatology, Palaeoecology* 138, no. 1–4: 27–42. https://doi.org/10.1016/S0031-0182(97)00130-2.

Popov, L. E., and R. M. Cocks. 2017. "Late Ordovician Palaeogeography and the Positions of the Kazakh Terranes Through Analysis of Their Brachiopod Faunas." *Acta Geologica Polonica* 67, no. 3: 323–380. https://doi.org/10.1515/agp-2017-0020.

Powell, W. 2003. "Greenschist-Facies Metamorphism of the Burgess Shale and Its Implications for Models of Fossil Formation and Preservation." *Canadian Journal of Earth Sciences* 40, no. 1: 13–25. https://doi.org/10.1139/e02-103.

Proctor, V. W. 1964. "Viability of Crustacean Eggs Recovered From Ducks." *Ecology* 45, no. 3: 656–658. https://doi.org/10.2307/1936124.

Rinkevičiūtė, S., R. Stankevič, S. Radzevičius, T. Meidla, A. Garbaras, and A. Spiridonov. 2022. "Dynamics of Ostracod Communities Throughout the Mulde/Lundgreni Event: Contrasting Patterns of Species Richness and Palaeocommunity Compositional Change." *Journal of the Geological Society* 179, no. 1: jgs2021-039. https://doi.org/10.1144/jgs2021-039.

Rosa, J., K. Martens, and J. Higuti. 2023. "Dried Aquatic Macrophytes Are Floating Egg Banks and Potential Dispersal Vectors of Ostracods (Crustacea) From Pleuston Communities." *Hydrobiologia* 850, no. 6: 1319–1329. https://doi.org/10.1007/s10750-022-04818-8.

Rubinstein, C. V., P. Gerrienne, G. S. de la Puente, R. A. Astini, and P. Steemans. 2010. "Early Middle Ordovician Evidence for Land Plants in Argentina (Eastern Gondwana)." *New Phytologist* 188, no. 2: 365–369. https://doi.org/10.1111/j.1469-8137.2010.03433.x.

Ruiz, F., M. L. González-Regalado, and J. M. Muñoz. 1997. "Multivariate Analysis Applied to Total and Living Fauna: Seasonal Ecology of Recent Benthic Ostracoda off the North Cádiz Gulf Coast (Southwestern Spain)." *Marine Micropaleontology* 31, no. 3: 183–203. https://doi.org/10.1016/S0377-8398(96)00060-6.

Salas, M. J. 2003. "Ostrácodos palaeocopas, leiocopas y eridostracas del Ordovícico de la Precordillera de San Juan, Argentina." *Ameghiniana* 40, no. 3: 345–360. https://www.ameghiniana.org.ar/index.php/ameghiniana/article/view/964.

Salas, M. J., and N. E. Vaccari. 2012. "New Insights Into the Early Diversification of the Ostracoda: Tremadocian Ostracods From the Cordillera Oriental, Argentina." *Acta Palaeontologica Polonica* 57, no. 1: 175–190. https://doi.org/10.4202/app.2009.1110.

Sarv, L. 1959. "Ordovician Ostracodes in the Estonian S.S.R." *Eesti NSV Teaduste Akadeemia Geoloogia Instituudi Uurimused* IV: 1–210. https://www.etera.ee/s/44RGBSyHwV.

Saupe, E. E., H. Qiao, Y. Donnadieu, et al. 2020. "Extinction Intensity During Ordovician and Cenozoic Glaciations Explained by Cooling and Palaeogeography." *Nature Geoscience* 13, no. 1: 65–70. https://doi.org/10.1038/s41561-019-0504-6.

Schallreuter, R. E. L. 1964. "Neue Ostracoden der Überfamilie Hollinacea." *Berichte der Geologischen Gesellschaft in der Deutschen Demokratischen Republik* 2: 87–148.

Schallreuter, R. E. L. 1968. "Drepanellacea (Ostracoda, Beyrichiida) aus Mittelordovizischen Backsteinkalkgschieben II. *Laterophores lateris* g. n. sp. n." *Pseudulrichia bucera (Neckaja) und Pedomphalella egregia (Sarv). Berichte der deutschen Gesellschaft fur geologische Wissenschaften Reihe A (Geologie und Paläontologie)* 13: 153, 155, 199, 247–261, 278–281.

Schallreuter, R. E. L. 1969. "Neue Ostracoden aus ordovizischen Geschieben, II (New Ostracods from Ordovician Boulders, II)." *Geologie* 18, no. 2: 204–215.

Schallreuter, R. E. L. 1971. "Ostrakoden aus Öjlemyrgeschieben (Ordoviz)." *Neues Jahrbuch für Geologie und Paläontologie (Monatsheft)* 7: 423–431.

Schallreuter, R. E. L. 1972. “Drepanellacea (Ostracoda, Beyrichiocopida) aus mittelordovizischen Backsteinkalkgeschieben IV: *Laterophores hystrix* sp. n., *Pedomphalella germanica* sp. n. und *Easchmidtella fragosa* (Neckaja).” *Berichte der deutschen Gesellschaft fur geologische Wissenschaften Reihe A (Geologie und Paläontologie)* 17: 139–145.

Schallreuter, R. E. L. 1983. “Zwei neue Ostrakoden aus einem mittelordovizischen Hornstein-Geschiebe der Insel Sylt (Two New Ostracodes From a Middle Ordovician Hornstone Erratic Boulder From the Isle of Sylt).” *Neues Jahrbuch für Geologie und Paläontologie (Monatsheft)* 1983, no. 10: 601–604. https://doi.org/10.1127/njgpm/1983/1983/601.

Schallreuter, R. E. L. 1984. “Geschiebe-Ostrakoden I.” *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen* 169: 1–40.

Schallreuter, R. E. L. 1986. “Ostrakoden aus Öjlemyrflint-Geschieben von Sylt.” In *Fossilien von Sylt II*, edited by U. V. Hacht, 203–232. Hamburg: Inge-Maria von Hacht Publishing House and Bookstore.

Schallreuter, R. E. L. 1987. “Ostrakoden aus ordovizischen Geschieben Westfalens 1.” *Geologie und Paläontologe in Westfalen* 7: 15–29.

Schallreuter, R. E. L. 1994. “Schwarze Orthocerenkalkgeschiebe.” *Archiv für Geschiebekunde* 1: 491–540.

Schallreuter, R. E. L. 1997. “Ostrakoden aus Tretaspiskalkgeschieben (Ordoviz) [Ostracodes From Geschiebes of Tretaspis Limestone (Ordovician)].” *Archiv für Geschiebekunde* 2, no. 3: 157–170.

Schallreuter, R. E. L. 2000. “Ostrakoden aus silurischen Geschieben IV.” *Geologie und Paläontologie in Westfalen* 53: 5–69.

Schallreuter, R. E. L., and I. Hinz-Schallreuter. 2010b. “Sexual Dimorphism and Pore Systems in Ordovician Ostracodes.” *Acta Palaeontologica Polonica* 55, no. 4: 741–760. https://doi.org/10.4202/app.2009.0056.

Schallreuter, R. E. L., and I. Hinz-Schallreuter. 2010a. “Synonyme von Geschiebe-Ostrakoden III (Synonyms of Ostracodes From Geschiebes III).” *Archiv für Geschiebekunde* 6, no. 1: 61–72.

Schallreuter, R. E. L., and I. Hinz-Schallreuter. 2011. “New Ostracodes From the Öjlemyr Chert (Late Ordovician) of Gotland and Northern Germany.” *Bollettino della Societa Paleontologica Italiana* 50, no. 3: 209–228. https://doi.org/10.4435/BSPI.2011.17.

Schallreuter, R. E. L., and I. Hinz-Schallreuter. 2013. “The Ordovician Ostracodes Established by Aurel Krause, Part II.” *Fossil Record* 16, no. 2: 145–169. https://doi.org/10.1002/mmng.201300007.

Schallreuter, R. E. L., I. Hinz-Schallreuter, M. Balini, and A. Ferretti. 2006. “Late Ordovician Ostracoda From Iran and Their Significance for Palaeogeographical Reconstructions.” *Zeitschrift für Geologische Wissenschaften* 34, no. 5: 293–345.

Schallreuter, R. E. L., I. Hinz-Schallreuter, A. Ferretti, and E. Serpagli. 2007. “Late Ordovician Ostracodes From Sardinia and Perigondwanan Ostracode Palaeobiogeography.” *Zeitschrift für Geologische Wissenschaften* 35: 253–331.

Schallreuter, R. E. L., and D. J. Siveter. 1985. “Ostracodes Across the Iapetus Ocean.” *Palaeontology* 28: 577–598.

Schieber, J. 2009. “Discovery of Agglutinated Benthic Foraminifera in Devonian Black Shales and Their Relevance for the Redox State of Ancient Seas.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 271, no. 3: 292–300. https://doi.org/10.1016/j.palaeo.2008.10.027.

Servais, T., T. Danelian, D. A. T. Harper, and A. Munnecke. 2014. “Possible Oceanic Circulation Patterns, Surface Water Currents and Upwelling Zones in the Early Palaeozoic.” *GFF* 136, no. 1: 229–233. https://doi.org/10.1080/11035897.2013.876659.

Sidaravičiene, N. 1992. *Ordovician Ostracods of Lithuania, Biostratigraphy*. Vilnius: Institute of Geology.

Siveter, D. J. 1984. “Habitats and Modes of Life of Silurian Ostracodes.” In *Autecology of Silurian Organisms*, edited by M. J. Bassett and J. D. Lawson, vol. 32, 71–85. London, UK: Palaeontological Association.

Siveter, D. J., D. E. G. Briggs, D. J. Siveter, and M. D. Sutton. 2010. “An Exceptionally Preserved Myodocopid Ostracod From the Silurian of Herefordshire, UK.” *Proceedings of the Royal Society B: Biological Sciences* 277, no. 1687: 1539–1544. https://doi.org/10.1098/rspb.2009.2122.

Siveter, D. J., G. Tanaka, Ú. C. Farrell, M. J. Martin, D. J. Siveter, and D. E. G. Briggs. 2014. “Exceptionally Preserved 450-Million-Year-Old Ordovician Ostracods With Brood Care.” *Current Biology* 24, no. 7: 801–806. https://doi.org/10.1016/j.cub.2014.02.040.

Siveter, D. J., J. M. C. Vannier, and D. Palmer. 1991. “Silurian Myodocopes: Pioneer Pelagic Ostracods and the Chronology of an Ecological Shift.” *Journal of Micropalaeontology* 10, no. 2: 151–173.

Song, J.-J., W. Guo, J.-Y. Huang, et al. 2022. “Silurian Ostracods From the Nyalam Region, Southern Tibet, China and Their Implications on Palaeoenvironment and Palaeobiogeography.” *Journal of Palaeogeography* 11, no. 1: 85–96. https://doi.org/10.1016/j.jop.2021.12.001.

Stocker, C. P., D. J. Siveter, P. D. Lane, et al. 2019. “The Paleobiogeographical Significance of the Silurian and Devonian Trilobites of Japan.” *Island Arc* 28, no. 2: e12287. https://doi.org/10.1111/iar.12287.

Sun, Q. 1988. “Ordovician Ostracoda From Western Hubei.” *Acta Micropalaeontologica Sinica* 5, no. 3: 253–266.

Tanaka, G. 2008. “Recent Benthonic Ostracod Assemblages as Indicators of the Tsushima Warm Current in the Southwestern Sea of Japan.” *Hydrobiologia* 598, no. 1: 271–284. https://doi.org/10.1007/s10750-007-9162-6.

Tanaka, H., M. Yasuhara, and J. T. Carlton. 2018. “Transoceanic Transport of Living Marine Ostracoda (Crustacea) on Tsunami Debris From the 2011 Great East Japan Earthquake.” *Aquatic Invasions* 13, no. 1: 125–135. https://doi.org/10.3391/ai.2018.13.1.10.

Teeter, J. W. 1973. “Geographic Distribution and Dispersal of Some Recent Shallow-Water Marine Ostracoda.” *Ohio Journal of Science* 73: 46–54.

Tinn, O., and T. Meidla. 2001. “Middle Ordovician Ostracods From the Lanna and Holen Limestones, South-Central Sweden.” *GFF* 123, no. 3: 129–136. https://doi.org/10.1080/11035890101233129.

Tinn, O., and T. Meidla. 2004. “Phylogenetic Relationships of Early–Middle Ordovician Ostracods of Baltoscandia.” *Palaeontology* 47, no. 2: 199–221.

Tong, D. T., T. H. Phương, P. Janvier, N. H. Hùng, N. T. T. Cúc, and N. T. Dương. 2013. “Silurian and Devonian in Vietnam—Stratigraphy and Facies.” *Journal of Geodynamics* 69: 165–185. https://doi.org/10.1016/j.jog.2011.10.001.

Tong, D. T., and K. Vu. 2011. *Stratigraphic Units of Viet Nam*. Second Edition—Revised and Updated. Hanoi: Vietnam National University.

Torsvik, T. H., and L. R. M. Cocks. 2013. “Chapter 2: New Global Palaeogeographical Reconstructions for the Early Palaeozoic and Their Generation.” *Geological Society, London, Memoirs* 38, no. 1: 5–24. https://doi.org/10.1144/M38.2.

Torsvik, T. H., and L. R. M. Cocks. 2016. *Earth History and Palaeogeography*. Cambridge: Cambridge University Press.

Trela, W. 2016. “Agglutinated Benthic Foraminifera in Ordovician and Silurian Black Mudrock Facies of the Holy Cross Mountains (Poland) and Their Significance in Recognition of Oxygen Content.” *Palaeogeography, Palaeoclimatology, Palaeoecology* 457: 242–246. https://doi.org/10.1016/j.palaeo.2016.06.015.

Trotter, J. A., I. S. Williams, C. R. Barnes, C. Lécuyer, and R. S. Nicoll. 2008. “Did Cooling Oceans Trigger Ordovician Biodiversification? Evidence From Conodont Thermometry.” *Science* 321, no. 5888: 550–554. https://doi.org/10.1126/science.1155814.

Vannier, J. M. C. 1986. “Ostracodes Binodicopa de I'Ordovicien (Arenig-Caradoc) ibéro-armoricain.” *Palaeontographica A* 193: 77–143.

Vannier, J. M. C. 1990. "Functional Morphology and Mode of Life of Palaeozoic Leiocope Ostracodes." *Lethaia* 23, no. 1: 103–112. https://doi.org/10.1111/j.1502-3931.1990.tb01785.x.

Vannier, J. M. C., D. J. Siveter, and R. E. L. Schallreuter. 1989. "The Composition and Palaeogeographical Significance of the Ordovician Ostracode Faunas of Southern Britain, Baltoscandia, and Ibero-Armorica." *Palaeontology* 32: 163–222. https://www.biodiversitylibrary.org/part/173943.

Vinn, O., M. A. Wilson, and U. Toom. 2015. "Distribution of Conichnus and Amphorichnus in the Lower Paleozoic of Estonia (Baltica)." *Carnets de Geologie* 15, no. 19: 269–278.

Vinyard, G. 1979. "An Ostracod (*Cypriodopsis vidua*) can Reduce Predation From Fish by Resisting Digestion." *American Midland Naturalist* 102, no. 1: 188–190. https://doi.org/10.2307/2425084.

Wang, S. Q. 2015. *Ordovician and Silurian Ostracoda of China*. Hefei: University of Science and Technology of China Press.

Wellman, C. H., P. L. Osterloff, and U. Mohiuddin. 2003. "Fragments of the Earliest Land Plants." *Nature* 425, no. 6955: 282–285. https://doi.org/10.1038/nature01884.

Whatley, R., and R. Jones. 1999. "The Marine Podocopid Ostracoda of Easter Island: A Paradox in Zoogeography and Evolution." *Marine Micropaleontology* 37, no. 3: 327–343. https://doi.org/10.1016/S0377-8398(99)00021-3.

Williams, M. 1990. "Ostracoda (Arthropoda) of the Middle Ordovician Simpson Group, Oklahoma, USA." Unpublished doctoral dissertation, University of Leicester.

Williams, M., J. R. Davies, R. A. Waters, A. W. A. Rushton, and P. R. Wilby. 2003a. "Stratigraphical and Palaeoecological Importance of Caradoc (Upper Ordovician) Graptolites From the Cardigan Area, Southwest Wales." *Geological Magazine* 140, no. 5: 549–571. https://doi.org/10.1017/S0016756803008057.

Williams, M., J. D. Floyd, C. G. Miller, D. J. Siveter, and P. Stone. 2000. "*Kinnekullea comma* (Jones, 1879), a Trans-Iapetus Ostracod Locum for the Late Ordovician *Dicellograptus anceps* Graptolite Biozone." *Journal of Micropalaeontology* 19, no. 2: 163–164. https://doi.org/10.1144/jm.19.2.163.

Williams, M., J. D. Floyd, M. J. Salas, D. J. Siveter, P. Stone, and J. M. C. Vannier. 2003b. "Patterns of Ostracod Migration for the 'North Atlantic' Region During the Ordovician." *Palaeogeography, Palaeoclimatology, Palaeoecology* 195, no. 1–2: 193–228. https://doi.org/10.1016/s0031-0182(03)00308-0.

Williams, M., and D. J. Siveter. 1996. "Lithofacies-Influenced Ostracod Associations in the Middle Ordovician Bromide Formation, Oklahoma, USA." *Journal of Micropalaeontology* 15, no. 1: 69–81. https://doi.org/10.1144/jm.15.1.69.

Williams, M., D. J. Siveter, M. J. Salas, J. M. C. Vannier, L. E. Popov, and M. Ghobadi Pour. 2008. "The Earliest Ostracods: The Geological Evidence." *Senckenbergiana Lethaea* 88, no. 1: 11–21. https://doi.org/10.1007/BF03043974.

Williams, M., P. Stone, D. J. Siveter, and P. Taylor. 2001. "Upper Ordovician Ostracods From the Cautley District, Northern England: Baltic and Laurentian Affinities." *Geological Magazine* 138, no. 5: 589–607. https://doi.org/10.1017/S0016756801005726.

Williams, M., and J. M. C. Vannier. 1995. "Middle Ordovician Aparchitidae and Schmidtellidae: The Significance of 'Featureless' Ostracods." *Journal of Micropalaeontology* 14, no. 1: 7–24. https://doi.org/10.1144/jm.14.1.7.

Witte, L., and D. van Harten. 1991. "Polymorphism, Biogeography and Systematics of *Kotoracythere inconspicua* (Brady, 1880) (Ostracoda: Pectocytheridae)." *Journal of Biogeography* 18, no. 4: 427–436. https://doi.org/10.2307/2845484.

Wong Hearing, T. W., A. Pohl, M. Williams, et al. 2021a. "Quantitative Comparison of Geological Data and Model Simulations Constrains Early Cambrian Geography and Climate." *Nature Communications* 12, no. 1: 3868. https://doi.org/10.1038/s41467-021-24141-5.

Wong Hearing, T. W., M. Williams, A. Rushton, et al. 2021b. "Late Ordovician (Katian) Graptolites and Shelly Fauna From the Phu Ngu Formation, North-East Vietnam." *Paleontological Research* 25, no. 1: 41–58. https://doi.org/10.2517/2020PR011.

Yang, S., W. Hu, and X. Wang. 2021. "Mechanism and Implications of Upwelling From the Late Ordovician to Early Silurian in the Yangtze Region, South China." *Chemical Geology* 565: 120074. https://doi.org/10.1016/j.chemgeo.2021.120074.

Zagora, K. 1968. "Ostracoden aus dem Unter-/Mittel-Devon von Ostthüringen." *Geologie* 17: 1–91.

Zhang, J., C. Li, X. Fang, et al. 2022. "Progressive Expansion of Seafloor Anoxia in the Middle to Late Ordovician Yangtze Sea: Implications for Concurrent Decline of Invertebrate Diversity." *Earth and Planetary Science Letters* 598: 117858. https://doi.org/10.1016/j.epsl.2022.117858.

Zhang, K., A. Yuan, and Q. Feng. 2018. "The Upper Ordovician Microfossil Assemblages From the Pagoda Formation in Zigui, Hubei Province." *Journal of Earth Science* 29, no. 4: 900–911. https://doi.org/10.1007/s12583-017-0958-7.

Zhang, T., W. Trela, S.-Y. Jiang, J. K. Nielsen, and Y. Shen. 2011. "Major Oceanic Redox Condition Change Correlated With the Rebound of Marine Animal Diversity During the Late Ordovician." *Geology* 39, no. 7: 675–678. https://doi.org/10.1130/g32020.1.

Zhang, Y.-C. 2023. "Late Darriwilian–Early Katian (Ordovician) Ostracods of Northeastern Yunnan, Southwest China." *Palaeoworld* 32, no. 2: 303–332. https://doi.org/10.1016/j.palwor.2022.04.002.

Zhao, Q., and P. Wang. 1988. "Distribution of Modern Ostracoda in the Shelf Seas Off China." In *Developments in Palaeontology and Stratigraphy*, edited by T. Hanai, N. Ikeya, and K. Ishizaki, vol. 11, 805–821. Elsevier. https://doi.org/10.1016/S0920-5446(08)70223.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.